FAUNAL AND FACIES DYNAMICS IN THE UPPER SILURIAN OF THE ANGLO-WELSH BASIN

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ABSTRACT. Faunal data are matched against major sedimentary facies to interpret benthic palaeoecology and palaeogeographical evolution through the Lower Leintwardine Formation (Ludlow Series, upper Silurian) of the Anglo-Welsh basin. In shelf areas, original patchiness of level-bottom benthic epifauna, opportunistic species, and wide faunal belts characterize the storm-influenced subtidal environments. Monospecific assemblages suggest high environmental stress. Breaks in shelf deposition, erosion, and hardground formation introduced the sequence, particularly in inshore areas, as carbonate shelf environments were replaced by clastic silt sedimentation. The most marked lateral faunal change, from skeletal benthos to graptolite assemblages, takes place across the offshore shelf margin, where tectonic controls are reflected in downslope slumping and submarine channelling. In low energy trough environments, scarcity of benthos other than infaunal lingulides suggests unfavourable bottom conditions. Leintwardinian faunas are subdivided broadly into three epifaunal brachiopod-dominated shelf associations, a brachiopod-ostracode offshore shelf assemblage, and a thanatocoenotic graptolite-lingulide trough association. Offshore spread of shelf environments in late Leintwardinian times was accompanied by immigration of new arthropod faunas, and shelf-wide domination by the distinctive Upper Leintwardine Formation association. Wider circulation patterns and regression heralded the final silting-up of the basin in response to late Caledonian tectonism.

THE Silurian depositional basin across the Welsh Borderland and Wales comprised an onshore platform area with a well-differentiated offshore trough to the west; the distribution of shelf and trough facies is well-established (e.g. Holland and Lawson 1963; Ziegler 1970). The narrow trough was aligned NE–SW through central Wales, although its present apparently linear axis and elongate configuration are somewhat accentuated by NW–SE Caledonian crustal shortening (min. 43 km: Coward and Siddans 1980). The closely defined stratigraphical framework for the Anglo-Welsh basin has allowed it to be a test area for palaeoecological research, following Ziegler's (1965) pioneer study. However, most surveys have covered broad stratigraphical ranges, and in relating faunal distributions to regional palaeogeography little attention has been given to substrate–organism relationships. This study focuses on a limited part of the sequence, the Lower Leintwardine Formation, and analyses in detail the faunas in relation to sedimentary facies.

Stratigraphical background. The Lower Leintwardine Formation is of late Silurian age (Ludlow Series, Ludfordian Stage) (Holland *et al.* 1959, 1963, 1980; Holland 1980). The boundary stratotypes for this formation and the overlying Upper Leintwardine Formation are in the Ludlow anticline, in shelly facies. The shelly faunal criteria thus strictly facilitate correlation only across the shelf region. In the graptolitic facies of trough areas, the Lower and Upper Leintwardine formations correlate with the *Saetograptus leintwardinensis* Biozone. Correlation of trough and shelf sequences relies on a limited graptolite distribution among shelf faunas and on reference to the transitional, mixed shelly and graptolitic faunas of shelf edge areas.

The main field transect runs SE–NW across the outcrop area, from shelf to basin (text-fig. 1). The Lower Leintwardine succession is considered in detail from the following sections: in shelf facies, from inliers at May Hill, N. Woolhope (Perton), the Malverns (Chances Pitch) and Abberleys (Woodbury), and in the main outcrop area from the type area of the Ludlow anticline; in the shelf edge region, from Aymestrey and Leintwardine; and in the trough, at Kerry. Complementary studies of parts of the sucession were made from the West Midlands inlier at Lye, in the Wenlock Edge district, Knighton, Lyepole Bridge, the Brecon anticlinal area, Builth, Usk, Llandovery—Llandeilo, and the Cennen Valley; sequences were also examined in the Dean and Brookend boreholes of the British Geological Survey.

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TEXT-FIG. 1. The major outcrop areas of Ludlow rocks, showing the main distribution of Leintwardinian rocks and key localities. The primary study sections (capitals) compose a shelf to basin transect (marked).

MAJOR FACIES TYPES

Three principal facies types are distinguished as a background to discussion of faunal distribution data: 1, Aymestry Limestone; 2, calcareous siltstone; and 3, laminated siltstone facies. The calcareous siltstone facies includes sequences dominated by sheet-laminated units and a more thickly flaggy variety. Locally, the laminated siltstone facies passes up through 'intermediate' sequences into this more thickly flaggy facies. The facies are described below, and are used on the stratigraphical range charts (text-figs. 5–12). Beyond the main transect, a fourth facies type, of poorly calcareous clastics, is distinguished for the SW of the outcrop area, and is used on palaeogeographical maps and sections (text-figs. 13 and 14). Conglomerates and phosphatized horizons within the major facies types are discussed separately.

1. *Aymestry Limestone facies*

The basal beds of the Lower Leintwardine Formation at the stratotype (SO 4953 7255) and across much of the shelf region are developed as carbonates within the top part of the Aymestry Limestone facies and its equivalents in shelf inliers. The major portion of the carbonate facies, however, belongs to the underlying Upper Bringewood Formation, in which facies variation was related by Watkins and Aithie (1980) to a west–east geographical gradient from high energy, shelf edge barrier environments (e.g. at View Edge, SO 4261 8071), to low energy, mud deposition in the back-barrier, inner shelf (e.g. at Woodbury, Frith Wood, and Perton; see text-fig. 1 for localities). Further south-east, such as at May Hill (Lawson 1955) and S. Woolhope (Squirrell and Tucker 1960), there is no carbonate sequence below the Lower Leintwardine Formation.

From the Ludlow anticline eastwards across the shelf inliers to Perton, the Aymestry Limestone of the Lower Leintwardine Formation comprises nodular, silty, and argillaceous limestones and calcareous siltstones. Terrigenous clay contents are high, and angular quartz silt forms a variable and commonly important component. Intense burrowing of the carbonate mud sediment is evident from the mottled, pelletal texture; this accounts for the destruction of much bedding fabric and for erratic mixing of skeletal grains through the strata. There are numerous fine-grained limestone (microsparitic) nodules, and local enrichment in carbonate is common. Nodule formation appears to have been early diagenetic, prior to compaction (Whitaker 1962; Watkins 1979). The nodular carbonates are irregular, in medium to thick units where bedding is picked out mainly by silty and shaly intercalations. The latter include bentonites, both in the basal Lower Leintwardine Formation and high in the Upper Bringewood Formation (text-figs. 5, 8, 9, 10; White and Lawson 1978). The lithologies of these sequences represent sediment dominated by mixed carbonate and terrigenous mud and silt, including limited amounts (mostly $< 10\%$) of skeletal material (= calcilutites of Jaanusson *in* Jaanusson *et al.* 1979; mudstones and wackestones of Dunham 1962), and deposited in conditions of low current energy. Beds of skeletal sand (calcarenites) among the muddy sediments are mostly mud-supported (wackestones), although there are also beds or lenses of variably sparitic deposits which are at least in part grain-supported (packstones). The latter, which have sharp lower contacts, represent intervals of higher current energy. The base of local units equivalent to the Lower Leintwardine Formation in the shelf inliers is placed at the appearance of conglomeratic beds among the skeletal calcarenites (e.g. Squirrell and Tucker 1960; Phipps and Reeve 1967); these conglomerates are discussed separately (p. 460).

There is a transition up into calcareous siltstone sequences, through nodular facies (e.g. Pl. 41; text-fig. 9) where calcareous siltstones replace limestones as the dominant lithology. This indicates increased silt influx in relation to carbonate deposition. Through this interval, thin biodetrital layers of fine skeletal sand together with some larger skeletal debris become common, as well as thicker, sparitic skeletal calcarenites, including conglomerates. The increased frequency of skeletal sands is accompanied by higher numerical abundance of the skeletal fauna.

West of Ludlow, in the shelf edge region at Shelderton, north of Leintwardine, and in the south-west part of Wenlock Edge, the Aymestry Limestone facies of the Lower Leintwardine Formation comprises higher energy carbonates. This trend corresponds to that shown by the underlying Upper Bringewood Formation. At Shelderton (SO 4157 7778), the upper part of the Upper Bringewood Formation is composed of thick, tabular, and cross-bedded sparitic calcarenites and crinoidal calcirudites (= grainstones), with thick interbeds of closely packed *Kirkidium knightii* valves. The sequence represents well-winnowed, grain-supported skeletal sands and gravels of high energy carbonate environments ('facies 6' of Watkins and Aithie 1980, as at View Edge). In this same area, at Lawnwell Dingle (SO 4163 7677), the basal Lower Leintwardine carbonates are dominantly thinner, nodular, silty skeletal calcarenites (= wackestones and packstones), passing up through transitional, highly nodular facies before muddy calcareous siltstones become the main lithology (text-fig. 11B). Beds throughout this sequence are crowded with the small articulate brachiopod *Dayia navicula*. Many basal skeletal layers are lenticular, although the thicker skeletal beds appear more laterally extensive and some pass up directly into flat-laminated, tabular sheets of hard calcareous siltstones. The sequence indicates fluctuating energy levels, with the winnowed skeletal sands representing numerous periods of strong current disturbance (such as storm waves) in an environment where carbonate and terrigenous mud and silt accumulated during intervals of quieter water conditions. By comparison with the coarse-grained, sparitic carbonates of the Upper Bringewood Formation, these basal Lower Leintwardine sediments represent a lowering of depositional energy levels.

Beyond the main transect, in the SW part of Wenlock Edge, the Lower Leintwardine Formation caps a pronounced limestone ridge (e.g. Shergold and Shirley 1968). Throughout the area the change within the Lower Leintwardine Formation up into calcareous siltstone facies is transitional (='basal—high Lower Leintwardine Beds' of Shergold and Shirley 1968). Lateral variation in the carbonate facies suggests higher depositional energy in the southern area, which is again comparable to the trend shown by the Upper Bringewood Formation. In the south (e.g. Norton Camp, SO 4451 8186), the Upper Bringewood carbonates are medium to thick, sparitic calcarenites which, by comparison with the Shelderton sequence, are somewhat finer grained and silty, and commonly contain a significant component of terrigenous clay. This suggests less turbulent environments for deposition of the skeletal sands, among which *K. knightii*, *Strophonella euglypha*, and corals are prominent (Greig *et al.* 1968). Watkins and Aithie (1980) interpreted sequences of this type as flanking, overwash deposits from the shelf edge bank environments (='facies 5'). The overlying basal Lower Leintwardine carbonates are mostly thinner, tabular calcarenites (wackestones and packstones), representing variably winnowed, mud- to grain-supported skeletal sands of moderate to high current energy. Towards the north-east, the Upper Bringewood carbonate sequences pass laterally into thinner bedded, siltier facies, a change which is reflected faunally in the absence of *K. knightii* and its replacement by a strophomenid-rich shelly fauna (e.g. 'strophomenid siltstone facies' of Holland and Lawson 1963, fig. 6). The basal Lower Leintwardine silty and muddy carbonates (e.g. north-west of Diddlebury, SO 4992 8688) include some tabular skeletal calcarenites, but there is a dominance of carbonate mud and silt deposition.

One further area where the basal Lower Leintwardine Formation is developed in carbonate facies is the West Midlands inlier at Lye (SO 930 845), where these beds belong to the top of the Sedgley Limestone (e.g. Holland *et al.* 1963). Thick, fine-grained and nodular Upper Bringewood limestones with shaly partings pass up into thinly bedded, skeletal limestones with siltstone interbeds, which have a Lower Leintwardine fauna (*c.* 2·4 m sequence; King and Lewis 1912). The limestones in this upper part are sparitic, commonly conglomeratic calcarenites (mostly packstones) representing winnowed skeletal sands and indicating conditions of high energy. They are interbedded with fine, muddy siltstones laid down in low energy environments. The sequence compares most closely with the conglomeratic intervals of SE shelf areas (p. 460).

Through most of the outcrop area of the Aymestry Limestone, the top part of the carbonate

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EXPLANATION OF PLATE 41

Figs. 1–6. Lower Leintwardine Formation facies. 1, nodular carbonates at top of Aymestry Limestone, Perton (SO 5952 3995). 2, sheet laminated siltstone unit in calcareous siltstone facies, Ludlow (SO 4893 7245), ×1·25; note erosional base to internal skeletal lens, and escape burrow trace (arrowed) from upper internal skeletal layer. 3, skeletal calcarenite in calcareous siltstone facies, Perton (SO 5952 3995), ×7·5. 4, isolated coarse siltstone sheet in transition from laminated siltstone facies to more thickly flaggy calcareous siltstone facies, Crickadarn (SO 0850 4258), ×1·25; note low angle lamination and erosional contact with underlying fine muddy siltstone; narrow *Chondrites* burrow traces are evident through the laminated bed. 5, *Lingula lata* valves in bedding surface assemblage, laminated siltstone facies, Lyepole Bridge (SO 4014 6530), ×3. 6, graded siltstone in poorly calcareous clastic facies, Cennen Valley (SN 6102 1906), ×15.

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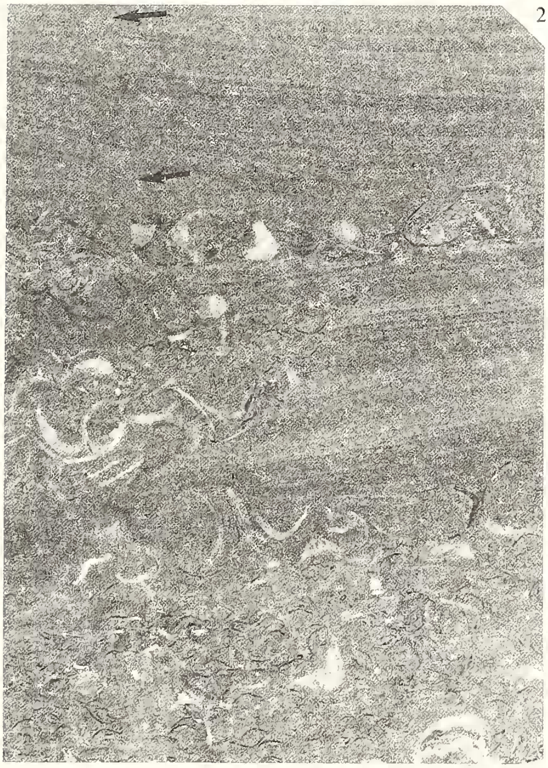

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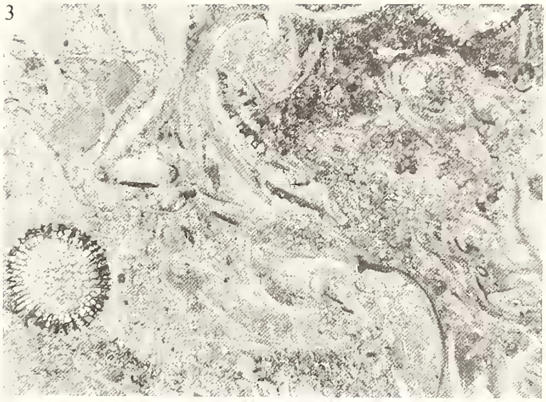

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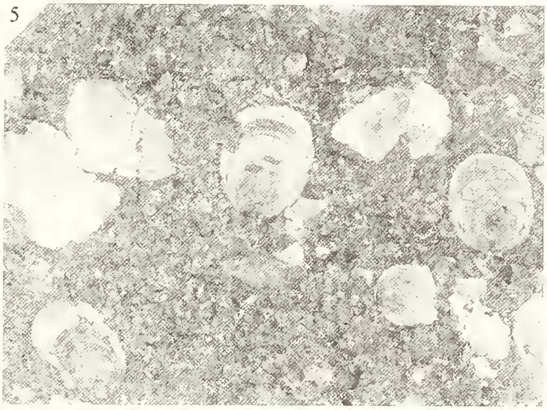

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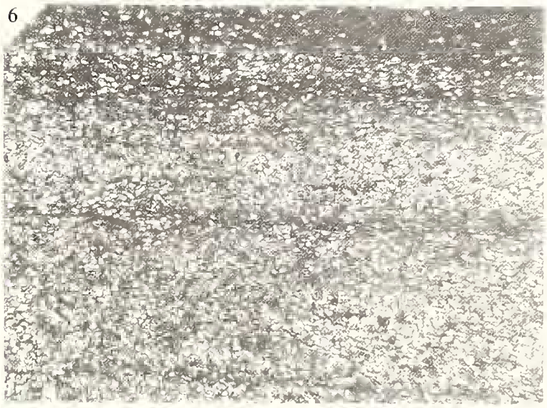


CHERNS, Lower Leintwardine Formation facies formation, which corresponds closely with the Upper Bringewood Formation–Lower Leintwardine Formation faunal boundary, is marked by increasing silt deposition and a general lowering of depositional energy levels, although there were interruptions of higher current energy when winnowed skeletal sands were deposited. The turbulent, barrier edge environments of the Upper Bringewood Formation were replaced by lower energy conditions, and some eastward migration of carbonate swell environments is evident in early Leintwardinian times before siliciclastic sedimentation became dominant across the whole shelf area.

2. *Calcareous siltstone facies*

The shelf sequences of the Lower Leintwardine Formation are predominantly thinly bedded clastic sediments, comprising carbonate-rich quartz siltstones, interbedded with thin carbonates that mostly represent layers or laterally impersistent lenticular concentrations of skeletal material. The sequences are richly fossiliferous; sediments are generally decalcified, so that shells are preserved as moulds. The siltstones are composed of medium to coarse, sub-rounded to angular silt, together with variable, but commonly high amounts of fine silt and clay and a low content of fine sand. Fresh samples have microspar carbonate cement, and the porous texture of decalcified areas suggests that most of these shelf sediments were previously calcareous. Some of the siltstones are finely laminated (individual layers < 1 mm), from carbonate-rich silts alternating with clay-rich and micaceous silts. In the thin micaceous laminae there are abundant, finely disseminated anhedral flakes of mica; in thicker bedded siltstones the content of mica, occurring as small flakes dispersed through the beds, is generally < 8%. Feldspars (potash) and other detrital minerals form only minor components (< 4%).

Bioturbation traces are widespread throughout the shelf succession, although a fairly high proportion of beds retain at least some primary bedding fabric. Among laminated sediments, branching networks of narrow, *Chondrites* traces are commonly evident, traversing bedding surfaces and passing shallowly and obliquely through the beds. More extensive deformative reworking by deposit feeders is indicated by beds with badly disrupted, remnant fabric or a patchy and mottled texture.

Skeletal material has an irregular distribution, mainly concentrated into layers of skeletal sand as micritic and sparitic calcarenites (Pl. 41). These deposits range from layers comprising a single blanket of shells to medium beds (> 15 cm), but typically they are thin (5–10 cm) and lenticular, representing bedding surface accumulations of shells which appear to extend up to only a few metres laterally. The thicker beds have sharply defined lower contacts but more transitional, silty, and bioturbated upper boundaries, grading up into calcareous siltstones. In some cases, it is evident that the skeletal bed forms the coarse basal layer of a sheet of laminated siltstone, with a rapid transition through finer skeletal debris up into the silt bed; these units are discussed separately below. Among the siltstones many beds include relatively few skeletal grains, and irregular mixing of small patches of skeletal sand appears to relate to burrowing activity. However, there are also beds in which skeletal material is common and widely distributed throughout, without the carbonate-rich matrix associated with shells that is typical of the skeletal calcarenites; these siltstones commonly have a rather homogeneous texture, indicating intense bioturbation.

The calcareous siltstone sequences represent sediment of carbonate-rich, muddy silts interbedded with mud- and grain-supported skeletal sands. Even in the micritic skeletal layers, mud left in intragranular cavities of skeletal grains indicates that the deposits are winnowed. The skeletal beds represent lag deposits resulting from episodes of higher current energy in an environment where silt-grade clastic material accumulated during lower energy intervals.

2*a*. *Sheet-laminated units*. This facies designation has been used to distinguish those parts of sequences in calcareous siltstone facies which include prominent beds of hard, flat-laminated calcareous siltstones, generally associated with basal skeletal concentrations. There is a marked regional variation in the distribution and nature of this facies (e.g. text-figs. 5–13). In the shelf inliers, beds of this type are thin (< 5 cm), and commonly the fabric of the siltstone portion is only patchily preserved because of bioturbation; it is reasonable to assume that many other, more extensively reworked beds in these sequences represent comparable deposits. (However, only where these units are well-developed through an interval of sediments has the facies been indicated on the range charts.) The main occurrence is in the Ludlow anticline, where medium units (mostly 10–15 cm) dominate the sequence in the middle Lower Leintwardine Formation (text-fig. 6B). Higher in the sequence, laminated units occur as isolated sheets and are mostly thinner (< 8 cm).

Text-fig. 6B shows a section at Ludlow (SO 4893 7245) where the lower part is dominated by thin to medium sheets of carbonate-rich, laminated siltstones, interbedded with thin, strongly bioturbated calcareous siltstones. The beds are richly fossiliferous. Individual units form flat-laminated, lenticular sheets (up to 20 cm, thickest centrally), extending up to a few metres across. The lamination, produced by alternation of silty and muddy layers, sometimes shows a rhythmite grading up through units, from coarser, silt-dominated into muddier, more finely laminated sediment. Individual laminae are generally < 1 mm although they locally reach 2–3 mm. The basal part of each unit is formed by closely packed, lenticular skeletal concentrations in carbonate-rich, mud-supported (more rarely grain-supported) calcarenites. The geometry of the sheets shows planar to gently undulating basal contacts that are sharp and commonly slightly erosional on beds beneath. Many of the thicker laminated sheets comprise multiple sets (up to a few cm thick), forming low-angle cross-strata infilling shallow troughs which each have coarse, skeletal basal layers (hummocky cross-stratification of Harms 1975). Some sheets display current ripple cross-lamination. Bioturbation of the top, muddy part of the units results in irregular silty patches which have a mottled, bioturbate texture, and the boundary with overlying thin siltstones is transitional. Within multiple units, the tops of individual sets also commonly show some burrow-disrupted fabric. However, in the main part of the laminated sheets, bioturbation traces are limited to a few, discrete escape burrows, steeply inclined to the bedding (e.g. Pl. 41; Watkins 1979, pl. 2).

In overall lithology, the laminated units do not differ significantly from interbedded siltstones, although the grading of the former means that the coarser basal layers contain a rather higher proportion of fine sand (< 10%) than is normal in the calcareous siltstones (< 5%). The composition of faunas in the laminated units and interbedded flags is discussed on pp. 469–473. The nature of the laminated units, with their slightly erosional basal contacts and coarse skeletal layers, suggests that they represent settling of suspension load by a waning current after a period of high current energy, comparable to Recent sheet deposits resulting from offshore transport of sediment by storm tidal and ebb currents (as documented from the North Sea, e.g. by Reineck and Singh 1980). The general lithological similarity to interbedded sediments suggests that these are fairly distal, open shelf deposits.

In the shelf edge region (e.g. at Lawnwell Dingle and south-west Wenlock Edge), the basal calcareous siltstone facies of the Lower Leintwardine Formation includes some thin (< 5 cm), finely laminated graded silt sheets. More prominent, isolated, laterally extensive tabular sheets of carbonate-rich siltstones with basal skeletal layers occur in the underlying Aymestry Limestone and transitional nodular carbonate facies in these sequences.

2*b*. *More thickly flaggy, calcareous siltstone facies.* A lithological change to more thickly flaggy sediments takes place in late Leintwardinian times at Ludlow and in some other areas further west. At the stratotype for the Upper Leintwardine Formation this transition occurs only in the uppermost metre of the higher division, and in other sections at Ludlow is above the important *Aegiria grayi–Neobeyrichia lauensis* faunal horizon (e.g. Lawson 1960); but at Leintwardine, Aymestrey, Brecon, and Builth it occurs below or close to this latter level. This facies continues in the overlying Lower Whitcliffe Formation in areas from Ludlow westwards (e.g. Holland and Lawson 1963, fig. 9: 'massively bedded').

The sediments are thin to mainly medium bedded, coarse- and medium-grained calcareous siltstones which display blocky or irregular fracture. Many beds have a homogeneous or burrow mottled texture, though others retain a laminated fabric. Isolated sheet-laminated deposits include ripple cross-laminated coarse siltstone/fine sandstone units, particularly among higher beds (e.g. Crickadarn Mill, SO 0850 4259). Skeletal material is commonly concentrated in thin layers of limited lateral extent among otherwise poorly fossiliferous beds, although sheet deposits may have prominent basal skeletal layers. The typical thin, decalcified seams with *grayi–lauensis* assemblages may occur separately from other, brachiopod dominated accumulations. At localities in the Leintwardine to Aymestrey region, some winnowed skeletal layers are associated with phosphatized pebble beds (e.g. text-fig. 11c).

The thickly flaggy calcareous siltstones represent mainly well-bioturbated silts of low to moderate energy environments, with intercalations of rapidly deposited, higher energy, laminated and sometimes micaceous silt/fine sand sheets that lie with flat, slightly erosional contact on underlying beds. Skeletal layers are winnowed current accumulations, and some thick and thinner skeletal layers associated with phosphatized material indicate periods of low net sedimentation and erosional reworking. However, the generally thicker beds suggest increased overall sedimentation rate compared with lower beds, and the silt sediment is somewhat coarser.

3. *Laminated siltstone facies*

The thick clastic sequences of the trough areas, which have limited, graptolitic faunas, comprise very thinly bedded, closely laminated siltstones interbedded with shaly, dark mudstones and fine siltstones (= 'laminated siltstone facies' of Holland and Lawson 1963). The proportions of muddy and silty lithologies vary both vertically and laterally; in general, shaly sequences are typical of western areas in the lower part of the succession, passing up transitionally into finely laminated siltstone sequences (e.g. Kerry, Clun Forest: Earp 1938, 1940). The laminated siltstones are fine to medium grained, slightly calcareous and muddy, with a narrow, parallel layering being produced by small differences in mean silt grade, carbonate, mica, and clay contents. Quartz grains are subrounded to angular, and comprise 30–40 % in a matrix of terrigenous clay with some microspar cement. Muscovite is a widespread minor detrital component, but occurs also in high concentrations of well-aligned, small anhedral flakes in some thin laminae. Opaque iron minerals occur in accessory amounts (< 2 %). Occasional thin beds of argillaceous calcilutite indicate that clastic sedimentation rate fluctuated. Minor current structures are evident in many beds. Thin laminae and shallow lenses of bioclastic debris and skeletal material have an irregular distribution among the siltstones, with inconspicuous layers of finely disseminated shell meal being rather more common than deposits of larger skeletal grains. The latter are mostly restricted to slump bands, both in western districts and in the intermediate, marginal shelf to trough areas of Builth, Cwm Graig Ddu (Straw 1937, 1953), and the Brecon anticlinal disturbance (Kirk 1951). The sparse, mainly planktic and lingulide faunas (e.g. Pl. 41; Cherns 1979) of the laminated siltstones contrast strongly with the shelly benthos of slumped beds. Among the laminated sediments, bioturbation traces are few or lacking.

Apart from minor local facies developments of silty, thinly bedded carbonates with Bringewoodian 'Aymestry Limestone' faunas in the Brecon region (e.g. Kirk 1951), fine clastic sediments dominate the trough succession through the Ludlow.

In the shelf edge areas of Aymestrey and Leintwardine (text-fig. 11), the very thinly bedded siltstones are rather more calcareous and fossiliferous, and with their mixed shelly and graptolitic faunas these sequences represent a transition between the calcareous siltstone facies of the shelf and the laminated siltstones of the trough. At Aymestrey, the laminated siltstones include some thin (< 3 cm) graded silt units which have skeletal basal layers, equivalent to the sheet-laminated deposits of the shelf sequences. There are also many thin, mud-supported skeletal calcarenites which represent winnowed shell accumulations. Patchy spreading of carbonate cement out from skeletal layers into adjacent sediments indicates diagenetic movement of carbonate.

The fine terrigenous muds and silts represented by the laminated siltstone facies were laid down in low energy environments. The restricted indigenous shelly benthos in trough areas, together with the reduced amount, or absence, of bioturbation suggests conditions inimical to most benthic organisms.

3a. 'Intermediate', laminated siltstone—more thickly flaggy, calcareous siltstone facies. The 'intermediate' facies occurs in the shelf edge region, through a transition from laminated siltstones up into more thickly flaggy calcareous siltstone facies in the higher Lower Leintwardine Formation (text-fig. 11A, C). The 'intermediate' sequence is mainly thinly bedded, medium–coarse, more calcareous siltstones, only some of which are laminated, and with harder very calcareous nodular beds and isolated laminated silt sheets (Pl. 41). In more fossiliferous sequences (e.g. at Shelderton; text-fig. 11C), as well as bedding surface skeletal layers there are beds with more dispersed skeletal material and homogeneous or mottled, bioturbate texture. However, in poorly fossiliferous sequences of similar lithology (e.g. Aymestrey; text-fig. 11A), few beds show traces of bioturbation and the sparse skeletal material is largely confined to occasional thin, impersistent, winnowed skeletal seams. The scarcity of fossils in intervening beds here suggests that epibenthic fauna was largely absent. The 'intermediate' facies represents deposition of coarser and less muddy silts, which in some areas were associated with an active endofauna, by contrast to the underlying laminated siltstone facies.

4. *Poorly calcareous clastic facies*

This facies refers to the thinly bedded and shaly mudstones, siltstones, and fine sandstones, with thin skeletal horizons, that comprise the Leintwardinian sequences of the SE flank of the Towy anticline in the south-west, Llandovery–Llandeilo region. It corresponds to the Cennen Beds of Squirrell and White (1978) and the Upper Cwm Clŷd Beds through Lower Roman Camp Beds of Potter and Price (1965) (e.g. at Sawdde Gorge). Towards the north-east this facies passes laterally into more argillaceous and very thinly bedded, commonly laminated and slightly calcareous sediments which make up the whole of the Cwm Clŷd beds (e.g. Clawdd British) and which are transitional into the laminated siltstone facies of the basin areas.

Characteristic of this facies type is the poorly or non-calcareous nature of the sediments (excluding skeletal layers). Coarser beds in thin section display tightly packed mosaics mainly of equigranular fine quartz sand or coarse silt. In the Cennen Valley the hard, coarser beds are dominantly of fine–medium sand grade, with angular to sub-rounded quartz grains that are separated by chloritic clay matrix, and with some layered fabric being picked out by more clayey laminae. Opaque iron minerals are a common accessory, and the decalcified skeletal layers appear ferruginous. Detrital mica occurs in minor amounts. In beds that have more tightly packed quartz mosaics the grains show sutured contacts. Small rounded shale or siltstone clasts and quartz gravel or coarse sand occur in some beds. At Sawdde Gorge, the sequence fines up overall into mainly siltstones (e.g. Pl. 41) and mudstones, but the basal, more sandy beds overlying the red, Bringewoodian Trichrûg Beds (Potter and Price 1965) also include some sharply based units of coarse quartz/small pebble conglomerates and tabular sandstones. The conglomerates have grains of rounded, sometimes polycrystalline quartz of coarse sand and gravel grade, small rounded rock particles (shale, siltstone, quartzitic sandstone), and rare pellets among finer, angular to sub-rounded quartz sand and silt in a reddish stained clayey matrix.

In the muddy layers and some laminated sandstones and siltstones, bioturbation traces are evident. Skeletal material is largely confined to thin and lenticular beds. By contrast to the Trichrûg Beds, where almost the only fauna is rare *Lingula* and *Orbiculoidea* found in thin grey beds thought to represent minor marine or estuarine incursions (Potter and Price 1965), the brachiopod-molluscan faunal assemblage of the overlying greenish grey beds is clearly marine.

These poorly calcareous clastic sequences appear to indicate deposition in low to moderate energy, marginal subtidal environments where mud and silt deposition alternated with influxes of coarser silt and sand, and where winnowed skeletal layers accumulated among the bioturbated muds as a result of minor current disturbances. Transgression over the deltaic Trichrûg deposits of Sawdde Gorge was followed by markedly lower energy sedimentation, albeit with storm episodes of stronger offshore currents which produced the conglomeratic beds among the basal cover.

Conglomerates

The stratigraphical range charts for localities along the main transect show that for shelf sequences (text-figs. 5–10), except in the type area of Ludlow, conglomeratic horizons occur widely around the Upper Bringewood–Lower Leintwardine boundary and in the lower part of the younger division, both in Aymestry Limestone facies and in calcareous siltstone facies. The base of local divisions equivalent to the Lower Leintwardine Formation in the shelf inliers is marked by conglomeratic beds (e.g. Lawson 1955; Squirrell and Tucker 1960; Phipps and Reeve 1967); the faunal data for this correlation are discussed below (pp. 474, 475). The interpretation of the conglomeratic horizons has been described elsewhere (Cherns 1980); widespread evidence for early lithification of carbonates and *in situ* hardground formation suggests that many of these beds represent prolonged breaks in sedimentation with episodic erosion, rather than the products of minor intraformational storm disturbances (cf. Watkins 1979) which dominate sedimentation higher in the Lower Leintwardine Formation.

In the south-east of the shelf, where the Aymestry Limestone is not developed, the lower part of the Lower Leintwardine Formation comprises conspicuous skeletal limestone conglomerates interbedded with fine, muddy calcareous siltstones and mudstones. The conglomeratic lower portion of the sequence thickens southwards from May Hill (text-fig. 7A; = Lower Blaisdon Beds of Lawson 1955) to the BGS Brookend borehole at Tites Point (e.g. text-figs. 1 and 14; Cave and White 1971). The underlying beds are muddy calcareous siltstones (May Hill) or mudstones (Brookend) with thin argillaceous limestones, which contain Bringewoodian shelly faunas (= Upper Flaxley Beds of Lawson 1955; Cave and White 1978). The thickest and coarsest beds of conglomerate occur in the basal Lower Leintwardine Formation (e.g. text-fig. 7A). These are sparitic skeletal calcarenites, containing well-rounded to elongated and flattened clasts of limestone and calcareous siltstone. Many clasts have bored and encrusted, corroded rims, and complex depositional histories (Cherns 1980, figs. 5–7). Where the distribution of bored clasts is closely associated with internal hardground surfaces, it appears that these lithified clasts subsequently became reworked only locally. In other beds, the thin, platy form of heavily bored clasts, and lack of abrasion of attached epizoan skeletons, also suggest only limited reworking. The high energy disturbances associated with the winnowed skeletal conglomerates alternated with low energy intervals during which interbedded fine, laminated clastic sediments were deposited. There is a strong contrast between the rich skeletal assemblages of these limestones and the otherwise generally sparse faunas (e.g. text-fig. 7A).

In the Aymestry Limestone and overlying calcareous siltstones of the shelf inliers (text-figs. 5–10, 13, 14), skeletal limestone conglomerates are common through the lower part of the Lower Leintwardine Formation. These beds represent winnowed, high energy concentrations of skeletal material, bioclastic debris, and commonly ill-sorted and variably rounded clasts of limestone and calcareous siltstone. In conglomerates from Perton, Woodbury, and Chances Pitch, borings are less numerous than in sequences further south. However, hardgrounds formed *in situ* in all these localities, mainly on carbonate sand substrates (e.g. Cherns 1980, fig. 7B, E). At Lye, the conglomerates include many bored calcarenite clasts but there is no evidence here for *in situ* hardening. It is apparent that comparable depositional conditions, involving intermittent sedimentation and episodic erosion, prevailed widely over the shelf areas in early Lower Leintwardine Formation times.

In the BGS Dean borehole (SO 678 000; Coppack and White 1974) on Wenlock Edge, in the northern shelf, there is a single conglomeratic horizon at the base of the Lower Leintwardine Formation, within well-bioturbated nodular argillaceous calcilutites and calcareous siltstones of the Aymestry Group. Here, *in situ* hardground formation affected carbonate mud sediment (Cherns 1980). At Aymestrey, near the shelf edge, Lawson (1973) reported a conglomeratic bed locally in the top of the Aymestry Limestone.

At Usk, Walmsley (1959) recorded a quartz conglomerate (25–35 cm thick) in temporary sections near Llandegveth in the extreme south of the inlier at around the base of the Lower Leintwardine Formation, i.e. in the lower part of the Upper Llanbadoc Beds. At one other locality, *c.* 2·4 km further north-east, he found a thin seam (*c.* 1·3 cm) with rounded quartz pebbles at this level, which he interpreted as the feather edge of a pebbly deposit derived from and thickening towards the south (also at Darran Plantation, ST 3276 9805: Squirrell and Downing 1969). The Llandegveth conglomerate (ST 3339 9603; ST 3332 9600), which cuts down erosively into the underlying calcareous siltstone, is grain supported, with rounded clasts of coarse sand to pebble grade, of quartz, quartzite, and volcanic rocks in a calcareous (sparitic) and shelly matrix that includes thelodont denticles (Walmsley 1959; Squirrell and Downing 1969). The quartz-rich composition of the Usk conglomerate contrasts with deposits in more easterly shelf inliers, and apparently relates to an unstable, southern source area. However, it indicates a depositional break also in the Usk region around the Upper Bringewood–Lower Leintwardine transition.

Phosphatized horizons

There are thin phosphatic horizons and matrix supported pebble beds at several localities high in the Lower Leintwardine Formation and close to the Upper Leintwardine Formation boundary, occurring in the thinly bedded calcareous siltstone facies of shelf sequences and in the more thickly flaggy facies of shelf edge sequences. In shelf areas, such beds occur at Longhope (text-fig. 7B), above the ?Lower Leintwardine Formation at the base of Whitcliffian strata at Gorsley (Lawson 1954), and at Perton (text-fig. 9; also Turner 1973). These beds are richly shelly or bioclastic with small rounded phosphatized clasts, thelodonts and acanthodian scales, and phosphatic (apatitic) skeletal fragments. Similar phosphatic pebble horizons or bone beds are also present at the top of the Upper Leintwardine Formation and in the Whitcliffian strata in these areas (Lawson 1955; Squirrell and Tucker 1960), and more widely, e.g. in the Brookend borehole, Tites Point, and Newnham inliers (Cave and White 1971), at the top of the Upper Leintwardine Formation at Usk (Squirrell and Downing 1969), and at the top of the Sedgley Limestone at Gornal (Ball 1951). At localities in the shelf edge region of Leintwardine there are horizons with worn and encrusted skeletal material (commonly large orthocones) high in the Lower Leintwardine Formation, and phosphatized pebble beds below the *grayi–lauensis* level (e.g. Shelderton; text-fig. 11C). These horizons are richly shelly siltstones, which include variably sized phosphatized clasts of muddy limestone. At Aymestrey there is a phosphatized conglomerate lower in the Lower Leintwardine Formation (text-fig. 11A), and then further thin phosphatized beds at the *grayi–lauensis* level (Lawson 1973). On Wenlock Edge Shergold and Shirley (1968) reported a ‘detrital limestone’ horizon at this higher level in the central/NE district.

The significance of the phosphatized pebble-bearing horizons lies in their indication of further periods of non-deposition and erosion, the derived clasts becoming phosphatized prior to burial. The most favourable conditions for deposition of phosphorites and phosphatization of sediment in platform settings are shallow warm seas, in areas with a low net sedimentation rate, and low energy environments where winnowing out of fine sediment results in enrichment of phosphatic material (e.g. review in Bromley 1967). At Shelderton (text-fig. 11C), closely spaced thin skeletal horizons which merge locally into prominent skeletal bands associated with worn and encrusted, derived material, indicate condensed sequences from episodic winnowing and reworking during periods of low net deposition. Both in the shelf inliers and shelf edge areas, the shelly faunas of the phosphatized beds are rich and diverse, clearly marine, and the occurrence of such beds within bioturbated and laminated silt sediments suggests that these are subtidal lag deposits.

SAMPLING AND RECORDING OF DATA

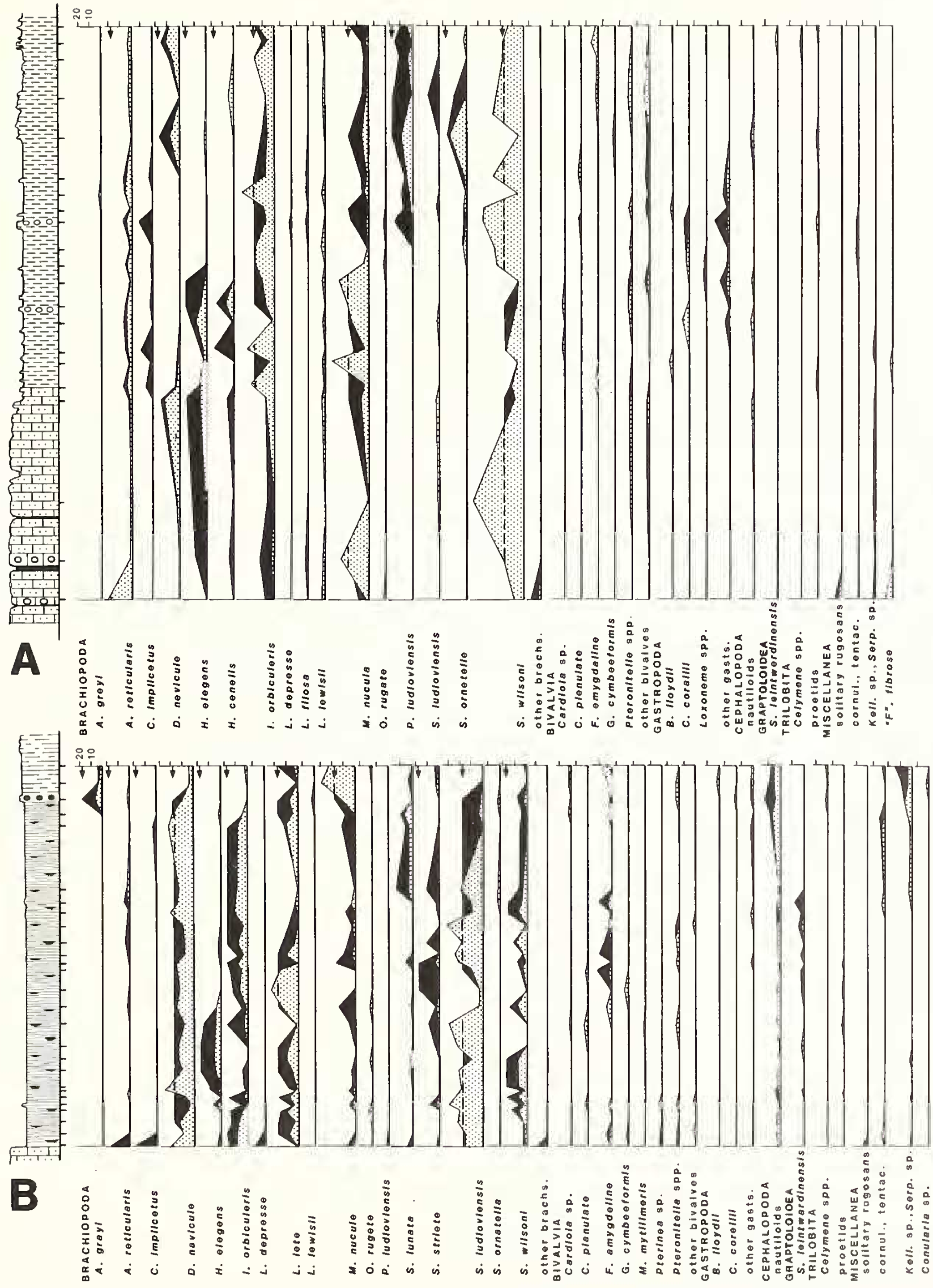
In Lower Leintwardine Formation shelly facies, skeletal material is characteristically concentrated into bands and lenses, with relatively little in intervening sediments. Also, there are considerable compositional differences between successive, and commonly narrowly spaced, assemblages, particularly in inner shelf sequences. Therefore, ‘spaced collection’ methods do not provide a representative record of the faunal pattern through a profile (cf. Calef and Hancock 1974; Watkins 1979), and bed-by-bed, continuous collecting was adopted for analysis of faunal composition and variation. Faunal records are based largely on field data, modified by subsequent laboratory examination of selected material. Full generic names of taxa discussed below are given in text-fig. 5.

Faunas were recorded qualitatively and semi-quantitatively, i.e. up to a maximum of eighteen individuals per species, for each unit, as follows:

> For bivalved macrofossils (brachiopods, bivalves), articulated specimens plus the greater number of either single valve and half the indeterminate valves. In shelf sequences, the majority of skeletal assemblages are dominated numerically by articulate brachiopods.
>
> All individuals and fragments of graptolites, gastropods, nautiloid cephalopods, solitary rugose and tabulate corals, tube-dwelling annelids (e.g. *Serpulites*, *Keilorites*), tentaculitids, and cornulitids. Since these groups form only minor components of shelly assemblages, the exaggeration of abundances inherent in including fragments is not important.
>
> For trilobites, complete individuals plus one-third of the total of pygidia and glabellae; smaller elements recorded as present (i.e. 1) only if these others were missing. The scoring represents a compromise between allowance for growth by ecdysis (e.g. Harrington 1959: individuals cf. total remains = perhaps 10 %) and the relative infrequency of the group.
>
> For bryozoans, encrusting and erect colonies plus half the fragments of ramose and bifoliate forms. Overestimation is chiefly important where fragmentation is high.
>
> For crinoids, articulated stem sections plus one-tenth of isolated ossicles were broadly estimated. This arbitrary fraction was taken with regard to the normal disintegration of the plated skeleton prior to fossilization being countered by the inconspicuous appearance of individual ossicles among skeletal assemblages. The records obtained are thus of limited application (Jaanusson 1984); thin section examination indicates a wider distribution than shown on the range charts, but echinoderms are generally no more than minor components of faunas above the Aymestry Limestone.
>
> For ostracodes, which belong with the meiofauna to small macrofauna (< 5 mm), a visual estimate was made of one-tenth of individuals and single valves. Counts were restricted to superficial examination of bedding surfaces and freshly cut faces of samples. The methodological problems in combining widely different size groups (e.g. meio- and macrofauna) in quantitative faunal analyses are discussed by Jaanusson (1984). Difficulties of *inter alia* effective sampling throw into question the reliability of results for small organisms such as ostracodes in an integrated study. The reduction factor applied makes some allowance for ecdysis (Benson 1961: 7–9 moults per individual) and also the trend of 'frequency dominance of the smallest' (Jaanusson 1979). The records shown are undoubtedly incomplete and a least approximation of abundance. Examination of skeletal sand in thin sections of carbonates shows a more ubiquitous distribution than the range charts indicate. However, in a series of limestone samples taken along the transect, although ostracodes are locally common (particularly non-palaeocopes) in shelf sequences they are generally only a minor component (< 5 %) of the skeletal sand, whereas among beds from higher Lower Leintwardine and Upper Leintwardine strata of the shelf edge region they form a quantitatively much more important fraction (up to 52 %). The field data also reflect this distributional feature (e.g. text-fig. 11c), since in the latter area ostracodes appear conspicuous among the limited skeletal faunas.

Collection size varied according to density of skeletal material, bed thickness and accessibility, and faunal composition. Representative samples of lithology and fauna were collected. There is sedimentological evidence for widely fluctuating rates of deposition locally within sequences, and regional thickness variations indicate differences between localities along the transect (e.g. text-fig. 14). Together with the heterogeneous distribution of fossils this means that standard volume does not provide an objective basis for data collection. Within localities the sample sizes were relatively consistent, so that individual range charts reflect absolute variations in local faunal abundance. However, particularly in the trough succession, where fossils are scarce, each sample took considerably longer to collect and thus abundances of taxa are exaggerated relative to the shelf data.

As a control on the sampling method, at Aymestrey and Woodbury Quarry parallel records of the first fifty macrofossils (except bryozoans, crinoid ossicles) in each sample were taken for comparison with the standard sampling method. Calef and Hancock's (1974) rarefaction graphs for May Hill Ludlow brachiopods show decreased rate of addition of new species by this sample size, and Watkins (1979) used fifty specimens for consideration of diversity and relative abundance within samples from Ludlow shelf sequences. The



TEXT-FIG. 2. Faunal records for the first fifty macrofossils counted (stippled area), superimposed on records from the standard sampling procedure (black), at A, Aymestrey and B, Woodbury (cf. text-figs. 11A and 10, respectively). The maximum, 'cut-off' level (arrowed) for the standard method is indicated (dashed line) where exceeded by the 'first fifty' record.

results obtained by the two methods (text-fig. 2) mostly show comparable quantitative variations in species abundance from bed to bed for the more common taxa. However, the 'fifty specimen' chart shows lower diversity in the fauna at a number of levels, indicating that this sample size was not always adequate with regard to more minor elements of faunas (also Watkins 1979, fig. 31E from the Lower Leintwardine Beds at Chances Pitch). More importantly, the limiting of data to macrofossils, which is implicit in taking a standard number of individuals, becomes increasingly inadequate to represent the fauna towards the shelf edge, where meiofauna—especially beyrichiacean ostracodes—form a quantitatively conspicuous component of many assemblages (e.g. text-fig. 11C). At Aymestrey, the striking difference between methods for the distributions of *Schizocrania striata*? is explained by the very inconspicuous appearance of the small, thin-shelled specimens, since the faunal records for this inarticulate brachiopod derive mainly from subsequent laboratory examination of material.

Limestone samples taken from the measured profiles were used for comparison of composition of skeletal sand with that of skeletal assemblages. Only limited results were obtained for the former because in recrystallized carbonates high proportions of grains are unidentifiable (commonly 25–50 %). Echinoderm abundances are probably least affected, since these particles retain relatively well-defined optical properties. Among the brachiopod-dominated sequences of shelf areas, articulate brachiopods also generally form the major component (commonly 40–50 %) of identifiable grains in the skeletal sand, with lesser amounts (10–20 %) of bryozoans and echinoderms, while molluscs, arthropods, and pellets form only minor components (mostly < 5 %). In the basal Lower Leintwardine Formation limestone conglomerates of the shelf inliers, bryozoans are conspicuous and locally become the dominant component of skeletal sand. In the shelf edge region, skeletal sand of richly shelly carbonates of the basal Lower Leintwardine Formation in Aymestry Limestone facies is dominated by brachiopods and echinoderms. There is a marked overall increase in brachiopod abundance by comparison with the underlying Upper Bringewood Formation in which, although brachiopod grains are commonly an important component (20–35 %), echinoderms (crinoids) are quantitatively dominant (40–70 %) in most beds (also Watkins and Aithie 1980). In the higher Lower (and Upper) Leintwardine of the shelf edge region, where arthropods become increasingly important in limited skeletal assemblages, the general decalcification of sediments limits compositional description to data from peels. In the thin skeletal layers, there is apparently relatively little fragmentation of many smaller skeletal grains, such as individual ostracode and *Aegiria grayi* valves, but brachiopods form the major component among associated shell debris.

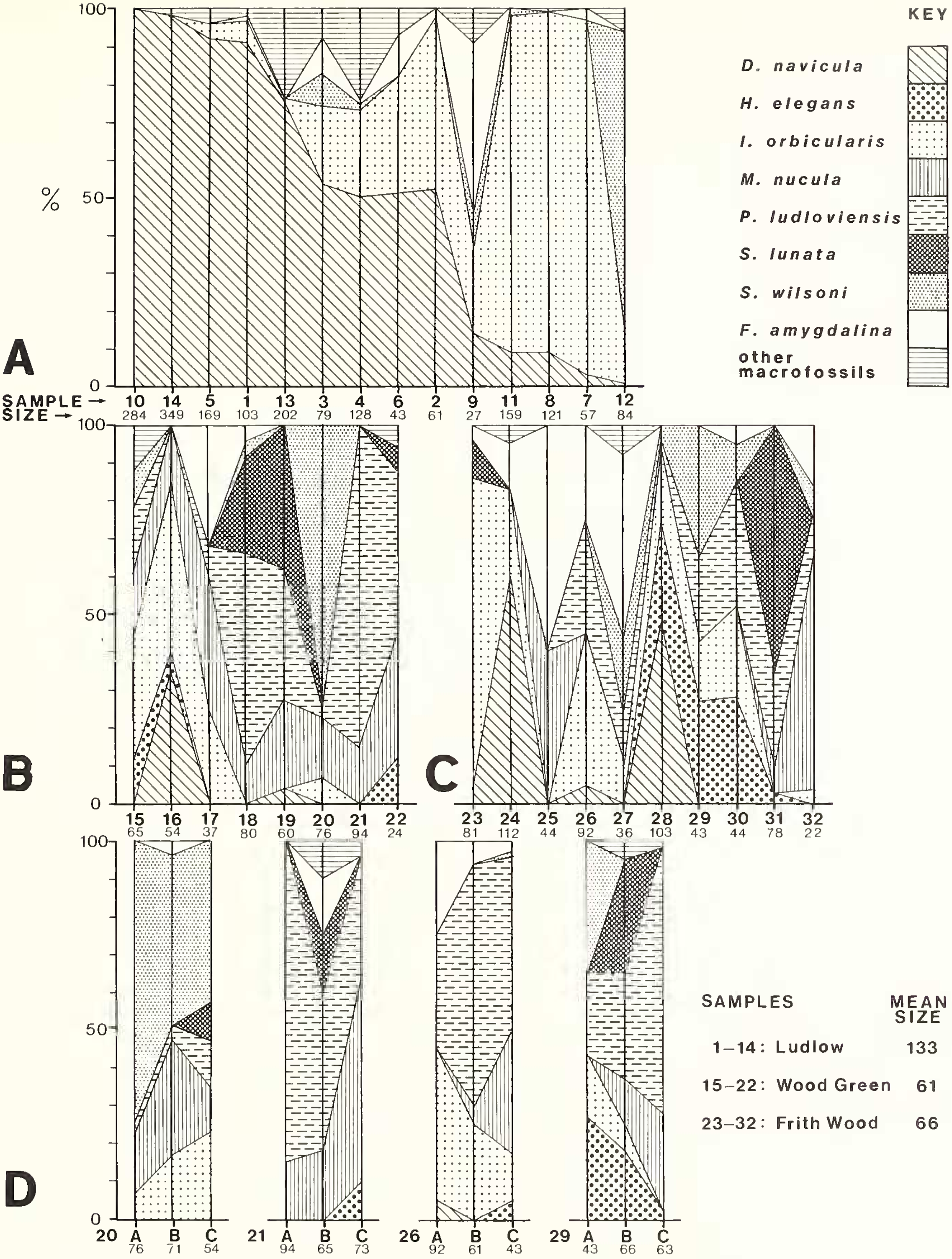
Raw faunal data for the stratigraphical range charts (text-figs. 5–12) are deposited with the British Library, Boston Spa, Yorkshire, UK as Supplementary Publication No. SUP 14033 (48 pages). They may be purchased from the British Library, Lending Division, Boston Spa, Wetherby, Yorks. LS23 7BQ. Prepaid coupons for such purposes are held by many technical and university libraries throughout the world.

SKELETAL DISTRIBUTION AND THE EFFECTS OF TRANSPORT

In the top part of the Aymestry Limestone facies and in the calcareous siltstone facies of the shelf, the main occurrence of skeletal material is in thin, laterally impersistent carbonate-rich skeletal layers. These occur at irregular but commonly narrow (< 2 cm) intervals. Intervening siltstones include finely laminated beds among others with patchy bedding fabric or a mottled texture, indicating bioturbational reworking. Beds with dispersed skeletal material are mostly well bioturbated. Burrowing activity appears to account for locally high fragmentation of shells and for some mixing of skeletal grains out from bedding surface assemblages, although many layers are little disturbed. Thinner skeletal beds are mostly mud-supported; they range from winnowed accumulations to assemblages of scattered shells. In thicker skeletal lenses the main concentration of shells is grain-supported, but peripheral parts of these same deposits are mud-supported. Sheet-laminated siltstones commonly have a marked basal skeletal bed sitting with sharp or erosional contact on beds below, and there are also thinner internal skeletal layers.

Calcareous siltstone facies, bedding surface assemblages

The nature of thinner skeletal layers was examined from sequences at Ludlow, Wood Green, and Frith Wood. Text-fig. 3 and Table 1 show the quantitative species composition of bedding surface assemblages within a 20 cm square quadrat.



TEXT-FIG. 3. Bedding surface assemblages (quadrat sites 400 sq. cm) from the Lower Leintwardine Formation at A, Ludlow (1–14; SO 4895 7240); B, Wood Green (15–22; SO 6945 1665); and C, Frith Wood (23–32; SO 723 404). D shows laterally adjacent sites for four bedding surfaces (20, 21, 26, 29). Sample sizes and means for the localities are given.

TABLE 1. Composition of bedding surface skeletal assemblages (20 cm square quadrat) at Ludlow (1–14; SO 4895 7240), Wood Green (15–22; SO 6945 1665), and Frith Wood (23–32; SO 723 404). The proportions of convex-up values (%), pedicle valves of *Isorthis orbicularis*, *Protochonetes ludloviensis*, and *Salopina lunata* (P%: populations ⩾ 20), and right valves of *Fuchsella amygdalina* (R%: populations ⩾ 15) are shown. ⌒, convex-up; ⌣, concave-up; t, min. total; T, max. total; P, pedicle valve; B, brachial valve; R, right valve; L, left valve.

		A		B		C		D	E		F		G	H		I		J	K	L	M	N	O	P
		D. navicula		H. elegans		I. orbicularis		M. nucula	P. ludloviensis		S. lunata		S. wilsoni	Other brachiopods		F. amygdalina		Other macrofossils	TOTAL	% convex-up	I. orbicularis %P	P. ludloviensis %P	S. lunata %P	F. amygdalina %R
Sample		P	B	P	B	P	B		P	B	P	B		P	B	R	L							
1. convex-up	⌒	35				6	2									1								
concave-up	⌣	56					1																	
min.	t	91				6		2								1			100					
max.	T	91				9		2								1			103	43.6				
2.	⌒	22				15	9										1							
	⌣	2					12																	
	t	24					21										1		46					
	T	24				46										1			61	77.0	32.6			
3.	⌒	32				6	3								1	6	2							
	⌣	3				8	7							1										
	t	35				14							6	1		6		4	66					
	T	35				24							6	2		8		4	79	72.5	58.3			
4.	⌒	26				12	14							25	12	1								
	⌣	26					10																	
	t	52					24						2	25		1			104					
	T	52				36							2	37		1			128	71.4	33.3			
5.	⌒	103				3	2							2										
	⌣	50					4																	
	t	153					6	5						2					166					
	T	153				9		5						2					169	67.1				
6.	⌒	2				10	2							1		1	4							
	⌣	16				1	5							1										
	t	18				11								2			4		35					
	T	18				18								2		5			43	46.5				
7.	⌒	1				24	20									1								
	⌣					2	9																	
	t	1					29									1			31					
	T	1				55										1			57	80.1	47.3			
8.	⌒	7				70	38																	
	⌣					4	1																	
	t	7				74		1											82					
	T	7				113		1											121	95.8	65.5			
9.	⌒	3					1									10	5							
	⌣						4																	
	t	3					5	2					2			10			22					
	T	3				5		2					2			15			27	82.6				66.7
10.	⌒	238																						
	⌣	46																						
	t	284																	284					
	T	284																	284	83.8				
11.	⌒	10				92	48																	
	⌣					7																		
	t	10				99							2						111					
	T	10				147							2						159	95.5	67.3			
12.	⌒					11	4							1										
	⌣					1	2																	
	t					12		3					62	1					78					
	T					18		3					62	1					84					
13.	⌒	136				1																		
	⌣	16												1										
	t	152				1		12						1				36	202					
	T	152				1		12						1				36	202	89.0				
14.	⌒	246												3	1									
	⌣	96																						
	t	342												3				3	349					
	T	342												4				3	349	72.2				
15.	⌒	5		3		3	13		7	4														
	⌣					4	1																	
	t	5		3			14	11	7				7					7	54					
	T	5		3		21		11	11				7					7	65	87.5	33.3			

TABLE 1 (*cont.*)

		A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P
16.	⌢	19	1	9 5													
	⌣		2	6 4													
	t	19		15	8							42					
	T	19	3	24	8							54	73.9	62.5			
17.	⌢			6 2		3				2 10							
	⌣			1													
	t			6	13	3				10		32					
	T			9	13	3				12		37	95.8				
18.	⌢					20 12	3 8			3							
	⌣					6 7	6 4										
	t				8	26	12	3		3		52					
	T				8	45	21	3		3		80	66.7		57.8	42.9	
19.	⌢	2				11 5	13 6										
	⌣	1				3 1	3 1										
	t	3			14	14	16					47					
	T	3			14	20	23					60	90.4		69.6	70.0	
20.	⌢			2 1		2											
	⌣			2													
	t			4	12	2		57				75					
	T			5	12	2		57				76					
21.	⌢					44 26											
	⌣					1 9											
	t				14	45						59					
	T				14	80						94	87.5			56.3	
22.	⌢		1 1			6 1	1										
	⌣		1			3 1											
	t		2		8	9	1				1	20					
	T		3		8	11	1				1	24					
23.	⌢			26 15			1 5			1 2							
	⌣	3		14 12			2										
	t	3		40			5			2		50					
	T	3		67			8			3		81	61.7	59.7			
24.	⌢	47 3		10 11						9 4							
	⌣	15 2		3 2													
	t	62		13						9	6	90					
	T	67		26						13	6	112	79.2	50.0			
25.	⌢									12 13							
	⌣									1							
	t				18					13		31					
	T				18					26		44	96.2				50.0
26.	⌢	2 1		17 6		8 12				16 5							
	⌣	2		13 1		1 6				2							
	t	4		30		18				16		68					
	T	5		37		27				23		92	72.8	81.1			69.6
27.	⌢			1		5				9 6							
	⌣			2 1						2							
	t			2		5		7		9	3	26					
	T			4		5		7		17	3	36	80.8		33.3		52.9
28.	⌢	36 4	11 10	12 8		2											
	⌣	10	6														
	t	46	17			2		4				81					
	T	50	27	20		2		4				103	83.8	60.0			
29.	⌢		7 4	1 5		6											
	⌣		1	1		1 2											
	t		8	6				15				36					
	T		12	7		9		15				43	82.1				
30.	⌢		7 2	6 4		7 7				2							
	⌣		3	1		1											
	t		10	7		8		4		2		31					
	T		12	11		15		4		2		44	87.5				
31.	⌢		2			13 7	30 9										
	⌣						8 4										
	t		2		5	13	38					58					
	T		2		5	20	51					78	83.6		65.0	74.5	
32.	⌢					2				4							
	⌣			1		1											
	t			1	12	2		2		4		21					
	T			1	12	3		2		4		22					

Most assemblages are numerically dominated by epifaunal articulate brachiopods, and apart from rhynchonellides the majority of shells are single valves. Bivalves are also locally important (e.g. samples 9, 25, 27: *Fuchsella amygdalina*), and typically are disarticulated. The resistance of shells to post-mortem disarticulation relates not only to energy of the environment and speed of burial, but also to hinge dentition and articulation. In brachiopods, the cyrtomatodont hinge (e.g. rhynchonellides) is more resistant to disarticulation than a deltidiodont one (e.g. orthides and strophomenides) (Jaanusson 1971). The length of exposure after death is a contributory factor, since retaining soft tissues decay rapidly; it follows that populations of conjoined deltidiodont brachiopods, or bivalves (where closure of the shell is controlled solely by soft tissues), were locally derived and quickly buried. Overall disarticulation ratios were not calculated because this would primarily reflect qualitative composition of assemblages. In general, rhynchonellides are more common among faunas at Wood Green (samples 15–22) and Frith Wood (samples 23–32), whereas Ludlow assemblages (samples 1–14) are dominated by *Dayia navicula* and *Isorthis orbicularis*.

The orientation of single valves (where common) among assemblages was used to calculate the proportions of convex-up to concave-up valves (Table 1). The convex-up orientation is dominant (> 67% in twenty-two of twenty-five assemblages). Preponderance of the hydrodynamically stable attitude (e.g. Brenchley and Newall 1970) indicates the effects of current transport on disarticulated shells, and possibly lack of much subsequent bioturbational reworking (e.g. Emery 1968).

The ratio of opposing valves was calculated for *I. orbicularis* and *Salopina lunata*, *Protochonetes ludloviensis*, and *F. amygdalina* (Table 1). This ratio has been suggested as a measure of current sorting, relating to commonly appreciable differences in size, shape, and weight between the two valves, and comparable to the right/left separation of bivalve shells along beaches (e.g. Boucot *et al.* 1958; Lever 1958; Craig 1967). The larger, pedicle valves are more common in the majority of the brachiopod assemblages. For *D. navicula*, where the two valves differ considerably, there are extremely few brachial valves (Table 1). Current sorting seems unlikely to explain the differential since no assemblages have the reverse composition. Differences in mechanical strength between dissimilar valves may be important, because small and thin shells become damaged and destroyed more quickly by turbulent conditions (Trewin and Walsh 1972). By contrast, current sorting may explain the markedly higher number of one valve in two out of four bivalve assemblages (samples 9, 17), although there is no apparent current alignment of shells.

There is rapid fluctuation in individual species abundance. Each assemblage characteristically has one or two numerically dominant species, and there is marked compositional variation from bed to bed. The total number of specimens per sample also varies widely, with the highest concentrations in virtually monospecific assemblages (e.g. samples 14, 10). The overall density of fossils is markedly higher at Ludlow (av. 120, cf. 61 and 65 per quadrat; samples 1–14; Table 1), where *D. navicula* and *I. orbicularis* show a generally inverse relationship in abundance although other species may dominate (e.g. sample 12, *Sphaerirhynchia wilsoni*; sample 9, *F. amygdalina*). These Ludlow assemblages illustrate the heterogeneity of faunas but are not representative of the relative proportions of assemblages in which the various individual species are prevalent. Successive faunas from Wood Green (samples 30–32) illustrate rapid faunal changes, the first having several common species, the next dominated by *Salopina lunata*, and then by *Microsphaeridiorhynchus nucula*. Composition and density of assemblages laterally show comparable variation, with considerable local differences (text-fig. 3; Table 2). For example, in sample 26 the numerically

TABLE 2. Lateral variation in quadrat assemblages, Wood Green (samples 20, 21; SO 6945 1665) and Frith Wood (samples 26, 29; SO 723 404).

Sample	20			21			26			29		
	A	B	C	A	B	C	A	B	C	A	B	C
Dayia navicula							4					
Howellella elegans			2			7			2	12	12	1
Isorthis orbicularis	5	12	12				37	15	5	7	4	
Microsphearidiorhynchus nucula	12	21	6	14	12	38		3	14		8	16
Protochonetes ludloviensis	2	3	6	80	27	24	28	38	20	9	19	2
Salopina lunata			5		10			2				
Sphaerirhynchia wilsoni	56	32	23						1	15	20	43
Fuchsella amygdalina		3			10	1	23	3	1			
Other macrofossils	1				6	3					3	1
Total	76	71	54	94	65	73	92	61	43	43	66	63

dominant *I. orbicularis* is replaced laterally by *P. ludloviensis* and is only a minor element in the third site, while the number of specimens per site ranges from ninety-two to forty-three.

The bedding surface layers represent concentrations of skeletal material, chiefly of benthic epifaunal organisms, and mostly occurring as disarticulated, convex-up shells. This suggests formation by periodic reworking of surface sediment and transport of skeletal grains. Since many shell beds are mud-supported and do not cut into beds beneath, current energy was only moderate and relatively little mixing and reworking have taken place. Assemblages retain an original heterogeneity in faunal distribution and are probably fairly locally derived. Resistance of shells to breakage decreases with exposure so that the generally low proportion of damaged shells (< 5%), together with the dominance of convex-up orientation and lack of evidence for much bioturbational disturbance, suggest rapid burial of skeletal assemblages.

Monospecific faunas

The wide fluctuations in species abundance from bed to bed result in many virtually monospecific assemblages (e.g. samples 14, 10: *D. navicula*). In more extensive, higher energy accumulations, including sheet-laminated units, the closely packed faunas are commonly of low diversity. Two major categories of skeletal distribution can be distinguished for these monospecific assemblages: type 1, skeletal concentrations in shell layers of variable thickness and extent; and type 2, a dispersed distribution of shells through beds. Populations of *D. navicula*, the two enteletaceans *I. orbicularis* and *S. lunata*, *Sphaerirhynchia wilsoni*, and *Shaleria ornatella* were analysed. As well as shell orientation and valve ratios, size frequency diagrams were constructed for populations.

Unfortunately, there is no general agreement on interpretation of size frequency data (e.g. see discussion in Williams *et al.* 1981). Many shell assemblages contain a relatively low proportion of small members. Few small specimens are also characteristic of many living brachiopod and bivalve populations (e.g. Rudwick 1965, 1970; Hallam 1967; Thayer 1975). However, the wide variation known from Recent forms prevents categorization of an original population structure; growth and mortality rates are highly variable (e.g. Hallam 1967), and recruitment can be patchy, irregular, and periodic (e.g. Jackson *et al.* 1971; Thayer 1975). In articulate brachiopods, where the free-living larval phase is short (e.g. Rudwick 1970), the occurrence of juveniles attached to adults (e.g. Thayer 1975; Curry 1981), prolonged brooding (e.g. McCammon and Buchsbaum 1968; Rickwood 1968), and polymodal size distributions (e.g. Craig and Hallam 1963; Jackson *et al.* 1971) suggest that dispersal of larvae is commonly limited. Reduction in the smaller size fractions is inherent both through selective removal by current action and because of relatively low fossilization potential, e.g. by solution and mechanical destruction (e.g. Hallam 1967; Curry 1981). Many common Lower Leintwardine brachiopods, such as *D. navicula* and *S. ornatella*, are pedically attached only in juvenile stages (p. 480), so that young individuals are particularly susceptible to removal; a comparable life strategy in bivalves involves the change from byssal attachment to free-living (e.g. Yonge 1962; Stanley 1970). For the size frequency data here, the absence of small forms is not taken alone as an indication of size sorting, but winnowing is extrapolated from variance relative to other populations, mean size, and from sedimentological and petrographical evidence.

D. navicula (text-fig. 4, samples 1–15). This species has its greatest abundance from Ludlow to the outer shelf. In the latter region these are the Dayia or Mocktree Shales of Elles and Slater (1906), and many assemblages through several metres of sequence are virtually monospecific. Populations were taken from calcareous siltstone facies at Ludlow (text-fig. 6B, both from sheet-laminated units and from the interbedded siltstones: samples 1–8), and from Aymestry Limestone facies in the Leintwardine area, from Shelderton (SO 416 778: sample 9) and Lawnwell Dingle (text-fig. 11B: samples 10–15).

Type 1 skeletal concentrations include: *a*, samples from sheet-laminated units from convex-up shell sheets which are evidently transported (samples 3A–D, adjacent sites from a single horizon; sample 4); *b*, closely packed current accumulations from interbedded siltstones (convex-up, sample 5; concave-up, samples 6, 7); *c*, grain-supported beds of convex-up shells from carbonate sequences (sample 12; samples 9A–C, sites from one bed); and *d*, mud-supported carbonates with variable shell orientation and many conjoined individuals (samples 13, 14; 65%, 50%, respectively). Where shells are in close contact and convex-up, disarticulation cannot be quantified since the hinge region of most shells is obscured. However, sections through shell layers suggest a high proportion of single pedicle valves, and concave-up assemblages (samples 6, 7) are almost entirely such. The distribution of convex-up shells in assemblages 3D–7 is indicated separately. The proportion of damaged shells is greater in highly concentrated assemblages (e.g. samples 9A–C, > 65%), and density of shells shows wide local variation (e.g. samples 3A–D, 65–91 individuals/quadrat, av. 75; samples 9A–C, 43–79 individuals/quadrat, av. 59).

Two type 1 assemblages are *e*, single shell thickness layers of limited lateral extent which have mainly unbroken, conjoined individuals (samples 8, 15; 75%, 70%, respectively) and large mean size compared with other populations (8·2 cf. 6·5 mm av. at Ludlow; 8·1 cf. 6·7 mm av. at Leintwardine); one (sample 15) has individuals predominantly with the umbo embedded in the sediment, apparently *in situ* (Tucker 1964).

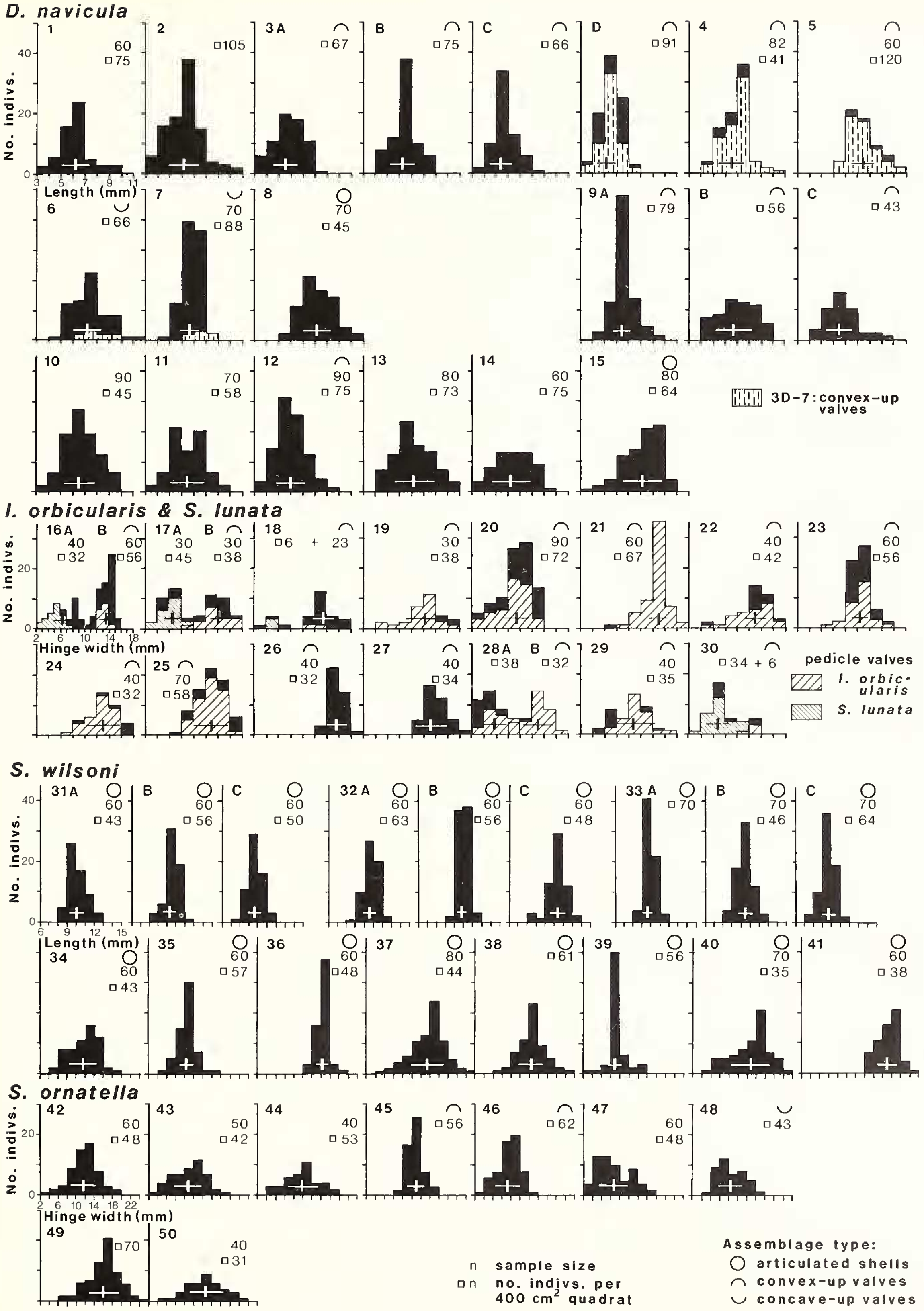
Type 2 assemblages of widely dispersed shells in siltstones (samples 1, 2, 10, 11) show a random distribution and orientation of skeletal grains. Poorly defined bedding fabric indicates biogenic reworking, but since there is little mixing outwards from intercalated skeletal layers the dispersed shells are probably locally derived. Damage from reworking is indicated by locally high fragmentation in areas of mottled, bioturbate texture.

The size frequency graphs show considerable variation, with as much variability within populations from a single current-derived bed as between beds (e.g. samples 9A–C, the χ^2 probabilities reject at 95% confidence level any pair having similar distribution). Small individuals are scarce, and there are very few brachial valves. Especially in high energy accumulations, relative fragility of these shells by comparison with the secondarily thickened, adult pedicle valves (e.g. Tucker 1968), and post-mortem removal of juveniles, seem likely explanations.

In both areas *D. navicula* is prevalent in type 1 transported, current accumulations of moderate to high energy environments but also occurs as locally derived populations in type 2 and some type 1 assemblages in interbedded sediments. This suggests that, either the higher energy deposits result from relatively local reworking of the surface sediment, or this faunal belt covered a wide area. At Ludlow, *D. navicula* is one of several prevalent species, and its abundance fluctuates rapidly from bed to bed. It occurs similarly in sheet-laminated and in interbedded siltstones. At Leintwardine this species has sole prevalence through the lower part of the succession. Disarticulation is high in both transported and locally derived, reworked assemblages. A large proportion of conjoined shells in some transported assemblages (samples 13, 14) suggests rapid burial.

I. orbicularis and Salopina lunata (text-fig. 4, samples 16–30). Valve ratios and orientations, as well as size frequency diagrams, were analyzed from enteletacean populations at Ludlow (samples 16–27), Wood Green (sample 28), and Frith Wood (samples 29, 30). More commonly, assemblages are dominated by one species (but cf. samples 16, 17); *I. orbicularis* occurs in abundance through the Lower Leintwardine shelf sequence, whereas *S. lunata* becomes increasingly common in the middle to upper part. Assemblages of either in type 1 transported accumulations are typically

TEXT-FIG. 4. Size frequency diagrams for articulate brachiopod populations of *Dayia navicula*, *Isorthis orbicularis* and *Salopina lunata*, *Sphaerirhynchia wilsoni*, and *Shaleria ornatella*. Means and standard deviations are shown, as well as sample size and number of individuals per quadrat, and type of assemblage (dominantly articulated shells, convex-up or concave-up valves). Samples: *D. navicula*, 1–8 = Ludlow (SO 4895 7240), 9 = Shelderton (SO 416 778), 10–15 = Lawnwell Dingle (SO 4163 7677); *I. orbicularis* and *Salopina lunata*, 16–27 = Ludlow (SO 4895 7240), 28 = Wood Green (SO 6945 1665), 29 and 30 = Frith Wood (SO 723 404); *Sphaerirhynchia wilsoni*, 31–34 = Perton (SO 5952 3995), 35 and 36 = Chances Pitch (SO 7475 4019), 37–41 = Woodbury (SO 7430 6368); *Shaleria ornatella*, 42–46 = Ludlow (SO 5071 7428), 47 and 48 = Woodbury (SO 7430 6368), 49 = Chances Pitch (SO 7486 4020), 50 = Perton (SO 5952 3995).


D. navicula
No. indivs.
0
20
40
1
60
□75
2
□105
3A
□67
B
□75
C
□66
D
□91
4
82
□41
5
60
□120
3
5
7
9
11
Length (mm)
6
□66
7
70
□88
8
70
□45
9A
□79
B
□56
C
□43
10
90
□45
11
70
□58
12
90
□75
13
80
□73
14
60
□75
15
80
□64
3D-7: convex-up valves
I. orbicularis & S. lunata
No. indivs.
0
20
16A
B
40
□32
60
□56
17A
B
30
□45
30
□38
18
□6 + 23
19
30
□38
20
90
□72
21
60
□67
22
40
□42
23
60
□56
2
6
10
14
18
Hinge width (mm)
24
40
□32
25
70
□58
26
40
□32
27
40
□34
28A
B
□38
□32
29
40
□35
30
□34 + 6
pedicle valves
I. orbicularis
S. lunata
S. wilsoni
No. indivs.
0
20
40
31A
60
□43
B
60
□56
C
60
□50
32A
60
□63
B
60
□56
C
60
□48
33A
□70
B
70
□46
C
70
□64
6
9
12
15
Length (mm)
34
60
□43
35
60
□57
36
60
□48
37
80
□44
38
□61
39
□56
40
70
□35
41
60
□38
S. ornatella
No. indivs.
0
20
42
60
□48
43
50
□42
44
40
□53
45
□56
46
□62
47
60
□48
48
□43
2
6
10
14
18
22
Hinge width (mm)
49
□70
50
40
□31
n sample size
□n no. indivs. per 400 cm² quadrat
Assemblage type:
○ articulated shells
◠ convex-up valves
◡ concave-up valves

single valves (> 90%), associated with variable amounts of fragmental debris. However, in some higher energy, carbonate-rich beds, a greater proportion of conjoined individuals (10–15%) suggests rapid deposition. Samples come from type 1 assemblages in *a*, prominent skeletal limestones (samples 19, 20, 29) and *b*, thin, bedding surface accumulations. At Ludlow, type 2 assemblages from beds of dispersed valves are interbedded with type 1 skeletal layers where convex-up orientations are dominant. There is a clear dominance of one valve in most assemblages (e.g. samples 21, 26, 27), which suggests current sorting. Difference in mean size reflects different hydrodynamic properties for the dissimilar valves. Discrete size frequency diagrams for mixed populations (e.g. for the two species in samples 16, 17, and for two laterally spaced populations of *I. orbicularis* in sample 28) indicate limited post-depositional winnowing, whereas low variance (e.g. samples 21, 23) indicates stronger reworking of some beds. At Ludlow, transported *I. orbicularis* assemblages form type 1 skeletal layers both in sheet-laminated units and interbedded siltstones. Thus, as with *D. navicula* there are no faunal grounds for differentiating these.

Sphaerirhynchia wilsoni (text-fig. 4, samples 31–41). The greatest abundance of the rhynchonellacean *S. wilsoni* is in the inshore shelf region. Populations were taken from Perton (samples 31–34), Chances Pitch (samples 35–36), and Woodbury (samples 37–41); at the first two, *S. wilsoni* composes many monospecific assemblages, while at Woodbury many skeletal bands dominated by *S. wilsoni* also include *M. nucula* (and vice versa). The type 1 skeletal concentrations are mostly lenticular, mud- to grain-supported carbonates, representing closely packed accumulations of shells up to several metres across. The mud-supported silty edges of these beds pass into more carbonate-rich, grain-supported sediment encompassing the main concentration of skeletal material. Thicker deposits have sparitic cement and much fragmental debris, indicating conditions of high current energy. Thinner, less conspicuous skeletal layers represent lower depositional energy levels. Even in high energy, well-winnowed skeletal beds there are many conjoined individuals, which indicates the strong articulation of the shell (p. 467).

All assemblages analysed are from type 1 skeletal beds. Samples from Perton and Chances Pitch are grain-supported concentrations: *a*, monospecific (samples 31–33, each with three lateral sites; samples 35, 36); and *b*, more diverse (sample 34: text-fig. 9, 77). From Woodbury, samples 37–41 are *c*, relatively thin, rhynchonellide (see above) shell layers (< 5 cm), from variably mud- to grain-supported sediment.

Size frequency graphs (max. length of the shell) show marked differences in population profile. Samples with low variance (samples 31–33, 35, 36, 39) appear to have undergone size sorting as a result of current action. For lateral sites of two beds (samples 31, 32) the low standard deviation for each implies that, despite variation in means of < 0·5 mm, there is a significant χ^2 difference between sites. This suggests sorting analogous to Recent shell banks (e.g. Lever and Thijsson 1968). Virtually monospecific assemblages could also result from extreme current sorting, or be an original distributional feature. The latter appears more probable, since rapid fluctuations in abundance of several common species, commonly without evidence of strong current energy or sorting, suggest an originally mosaic distribution of species.

The assemblages from Woodbury, which have larger mean size (12·6 mm, cf. 10·4 mm at Perton), differ widely in variance (e.g. samples 37, 40, cf. 39). Beds are mud-supported, which suggests lower depositional energy environments than at the other localities. Although somewhat equivocal, unless the lower contacts of beds are clearly erosional there is no evidence that assemblages of conjoined shells have been transported far; type 1 skeletal layers which comprise small 'clusters' of shells and fragmental material among the calcareous siltstones may represent very locally derived populations.

Shaleria ornatella (text-fig. 4, samples 42–50). This stropheodontide has its main abundance in shelf facies of the Upper Leintwardine Formation (e.g. Lawson 1960), although it is also locally common at scattered horizons lower in the sequence in these areas and becomes a major faunal element of the lower division in the east of the Ludlow anticline (text-fig. 5). Many assemblages comprise closely packed, single valves in bedding surface accumulations.

Populations were taken from Lower Leintwardine shelf strata (Ludlow, samples 42–46; Chances Pitch, sample 49; Perton, sample 50), and across the Lower–Upper Leintwardine boundary (Woodbury, samples 47, 48; = text-fig. 10: 49, 50 respectively). Samples from type 1 assemblages include *a*, fairly diverse, brachiopod-dominated limestone faunas (samples 43, 50), and *b*, monospecific assemblages from thick beds of tightly packed and imbricated valves (samples 44, 47, 49). These imbricated assemblages and mixed faunas represent winnowed, higher energy deposits, at least in part grain-supported and associated with much fragmental debris. There are also *c*, monospecific assemblages from thin layers of bedding-parallel valves (samples 45, 46, 48).

Convex-up/concave-up ratios (samples 45, 46, 48) indicate no major preferred orientation, and little difference in the numbers of pedicle and brachial valves. The greater concentrations in higher energy deposits include sheet-laminated units (samples 43, 44) which were apparently rapidly buried. A type 2 dispersed population (sample 42), which represents a low energy, local deposit, shows normal distribution and wide variance.

At Ludlow (text-fig. 5), *S. ornatella* forms many type 1 transported current accumulations, but its occurrence in interbedded sediments as more locally derived type 2 assemblages indicates that it was also indigenous here. This distribution pattern is characteristic right across the shelf area in the Upper Leintwardine sequences. In the lower part of the Lower Leintwardine Formation, the species is abundant only in local horizons, in transported type 1 accumulations of skeletal limestones (e.g. text-fig. 6, samples 30–40; text-fig. 5, samples 19–23). Then, both *S. ornatella* and the other stropheodontide *Leptostrophia filosa* are essentially restricted to higher energy deposits and are infrequent in interbedded siltstones. A similar pattern is seen also at Perton (text-fig. 9, samples 30–38). This suggests that the assemblages may have become introduced into these areas periodically; stropheodontides are unattached, and the wide, flat and light, easily disarticulated shells appear susceptible to current scour.

Analysis of monospecific faunas of five brachiopod species among calcareous siltstone facies indicates variable reworking and levels of current energy. For *D. navicula*, *I. orbicularis*, and *Salopina lunata*, monospecific populations of largely single valves in higher energy, type 1 deposits are interbedded with similar assemblages of types 1 and 2 in less reworked beds, and for *D. navicula* there are even some local, articulated populations. Lack of faunal distinction between prominent sheet laminated siltstone units and interbedded siltstones is a possible indication of wide faunal belts. For *Sphaerirhynchia wilsoni*, where shells typically remain conjoined, rigorous reworking of some accumulations is deduced from size frequency distributions. Again, other assemblages in the same sequences are current derived deposits of lower energy, and there is no indication of extensive faunal mixing as a result of transport. For *Shaleria ornatella*, which occurs as disarticulated valves, a wide faunal belt is apparent in the acme for the species in high Lower Leintwardine–Upper Leintwardine strata. The more limited and local occurrences of this stropheodontide and also *L. filosa* lower in the Lower Leintwardine Formation, restricted to well-winnowed accumulations, may represent non-indigenous faunas introduced by more extensive transport. They could, however, also be interpreted as temporary faunal shifts.

The occurrence of monospecific brachiopod faunas is important in its indication of environmental stress. Such assemblages are uncommon in Recent level-bottom communities, where articulate brachiopods show slow growth and low recruitment, and hence poor competitive ability (e.g. Thayer 1981). By contrast, the Silurian faunas suggest 'opportunistic' species distribution; articulate brachiopods dominated the majority of assemblages and the monospecific assemblages indicate rapid, temporary expansions in population size.

Laminated siltstone facies, bedding surface assemblages

In the laminated siltstone facies there is a pronounced difference in skeletal distribution between the offshore shelf, Aymestrey to Leintwardine region and those areas further to the west. However, in all sequences the finely laminated fabric of many sediments indicates a lack of bioturbational reworking.

At Aymestrey the skeletal assemblages of the lower part of the Lower Leintwardine Formation are characteristically thin, impersistent bedding surface accumulations of disarticulated shells, ranging from closely packed, imbricated deposits, through single layer shell blankets to widely dispersed skeletal grains. Convex-up orientation is greatly dominant, and a number of the low diversity assemblages also show preferred alignment of skeletal grains. (For example, all one assemblage of twenty-two *F. amygdalina* valves are convex-up, right valves dominate 17:5, and seventeen lie with the long axis aligned within one 30° interval ENE–WSW; in this same bed scour grooves have the same alignment.) Degree of breakage is variable, but preservation of the delicate hinge spines of *Shagamella ludloviensis* pedicle valves, and unbroken valves of the thin shelled *Lingula lata* and small *Schizocrania striata*?, indicate only moderate water energy and reworking. Low diversity and local species prevalence are typical of the brachiopod and bivalve dominated assemblages, and appear to represent an original distribution feature. Graptolites occur commonly in some beds, including assemblages of aligned rhabdosomes, and occasionally together with *L. lata* valves.

At Lyepole Bridge quarry (SO 4014 6530), *c.* 2·2 km west of Aymestrey, and west of the outcrop area of the Aymestry Limestone, very thinly bedded and shaly, dark laminated siltstones are interbedded with thin units (< 1 m) of slumped strata which appear to be derived from the south-east. In the interbedded undisturbed siltstones, where skeletal material is mainly confined to very thin bedding surface layers, the ‘indigenous’ fauna is mostly *L. lata* valves and graptolites. Both these form monospecific bedding surface assemblages but they also occur together. Graptolite assemblages include some with aligned rhabdosomes; *L. lata* assemblages range from widely scattered valves to densely packed layers of single valves several shells thick, and much of the breakage appears due to post-depositional compaction (e.g. Cherns 1979). These assemblages, though current derived, are of low to moderate energy environments. By contrast, the slumped beds have closely packed, thick shelly deposits dominated by articulate brachiopods (especially *D. navicula*) and associated with much bioclastic debris. These faunas presumably derived, along with the slumped beds, from areas higher up the depositional slope.

Further west in trough areas, where faunas are considerably sparser, the faunal distribution is similar and shelly assemblages are largely restricted to slumped sequences.

BIOSTRATIGRAPHY OF THE LOWER LEINTWARDINE FORMATION

Base of Lower Leintwardine Formation

Holland *et al.* (1963) placed the base of the Lower Leintwardine Formation within the top of the Aymestry Limestone facies at the stratotype (text-fig. 5). The boundary is essentially coincident with a level characterized by the loss of diagnostic Upper Bringewood fossils; many of the common Lower Leintwardine forms are long-ranging species and continue from the older formation. The Upper Bringewood indices include *Kirkidium knightii*, *Amphistrophia funiculata*, *Gypidula lata*, *Strophonella euglypha*, tabulate corals, *Dalmanites myops*, and *Poleumita globosa* (e.g. Lawson 1960).

At Ludlow, faunas are commonly sparse through the boundary interval and dominated numerically by the brachiopods *Atrypa reticularis* and *I. orbicularis*. Through to the top of the carbonate unit, species diversity and abundance of macrofossils increase. The lithological transition up into calcareous siltstone facies is more distinct at the stratotype than in more westerly sections (text-fig. 6A).

In the shelf inliers, the base of the Lower Leintwardine Formation is placed well below (*c.* 5 m) the top of the Aymestry Limestone at Woodbury (text-fig. 10), within transitional facies at the top of the carbonate development at Chances Pitch (text-fig. 8; = Aymestry Limestone Member of Phipps and Reeve 1967 at these two localities), and below a transition (*c.* 4·5 m) through nodular carbonate facies at Perton (text-fig. 9; = Upper Sleaves Oak Beds of Squirrell and Tucker 1960). (In the stratigraphical range charts, dominance of calcareous siltstones within the transitional facies is taken to denote calcareous siltstone facies.) The faunal changes span several metres through poorly fossiliferous beds, and correspond closely to the incoming of shelly conglomeratic limestones. At Chances Pitch and Perton the boundary can conveniently be taken at the lowermost conglomerate, but since at Woodbury the equivalent horizon contained a typically Upper Bringewood fauna the boundary here was placed at a conglomerate *c.* 2 m higher where Upper Bringewood fossils are no more than rare. The sparse fauna of the topmost Upper Bringewood beds is dominated by *A. reticularis*, with some diagnostic Upper Bringewood forms.

In south-eastern shelf areas where there is no carbonate formation in the Ludlow Series, faunal changes at the base of the Lower Leintwardine Formation also correspond to the incoming of prominent limestone conglomerates, among muddy calcareous siltstone sequences (e.g. Lawson 1955; Cave and White 1971). The diverse brachiopod–bryozoan faunas of these limestones replace Bringewoodian strophomenid–coral faunas, and only rare Bringewoodian indices are found above this level (e.g. text-fig. 7).

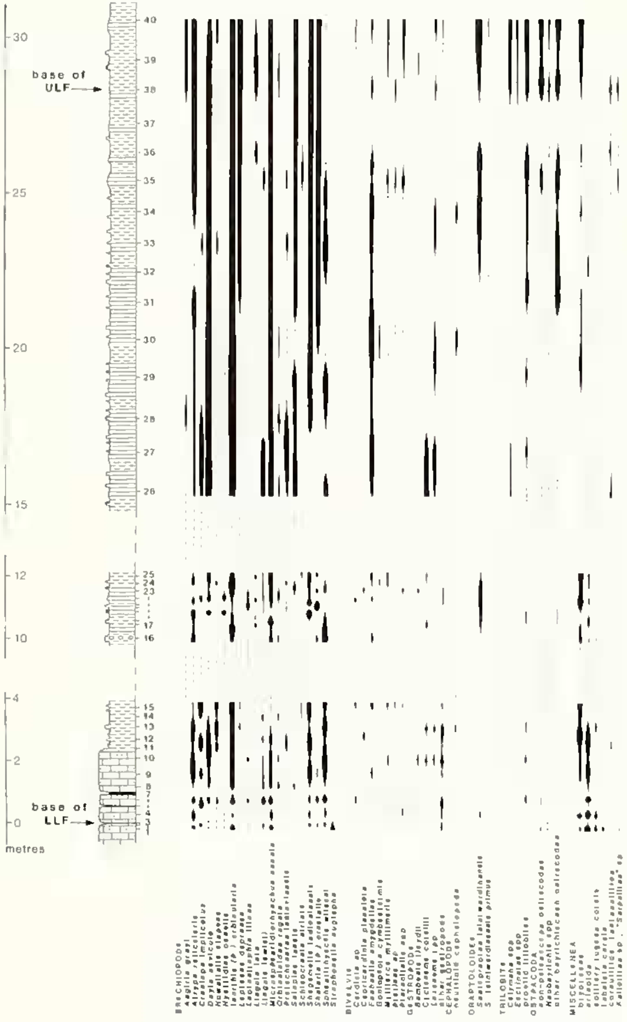
To the west from Ludlow, in the Leintwardine and Wenlock Edge districts, the base of the Lower Leintwardine Formation locally occurs well within the Limestone. In the classic area for the 'Dayia shales' of Elles and Slater (1906) the base of the Lower Leintwardine Formation is placed at the faunal change from the characteristic high-energy Upper Bringewood assemblage of the massive 'Conchidium Limestone' (p. 453) into the *Dayia* rich beds. The section from Lawnwell Dingle (text-fig. 11B) starts in very fossiliferous basal Lower Leintwardine beds *c.* 1–2 m above the boundary. In the south-west part of Wenlock Edge, the boundary is a similar marked faunal change up into rich and diverse small brachiopod associations. As well as *D. navicula*, *A. reticularis*, *I. orbicularis*, *Sphaerirhynchia wilsoni*, *M. nucula*, *Shagamella ludloviensis*, *Howellella elegans*, and *Hyattidina canalis* are also very common. North-eastwards, in the siltier facies of the Aymestry Limestone, strophomenid-rich Upper Bringewood assemblages are replaced by brachiopod faunas dominated by *A. reticularis*, *Sphaerirhynchia wilsoni*, *I. orbicularis*, *Howellella elegans*, and *M. nucula*.

In shelf edge districts, the base of the Lower Leintwardine Formation corresponds to a sharp lithological change at the top of the Aymestry Limestone (e.g. text-fig. 11A). In south Shelderton (e.g. Bow Bridge, SO 4304 7314) laminated siltstone facies lies with sharp but apparently conformable contact on thick, nodular Upper Bringewood limestones. The lowermost siltstones include rich, monospecific concentrations of *D. navicula* and *I. orbicularis* valves. At Aymestrey (text-fig. 11A), the top of the Limestone is locally an erosional planed surface (cf. Lawson 1973). There are truncated fossils, and surficial shallow, silt and clay filled, weathered pits. Winnowed skeletal layers with abraded limestone pebbles and Upper Bringewood fossils form lag deposits. In a nearby track section (SO 4190 6558), Lawson (1973) noted a conglomeratic bed (20 cm) in the top of the Limestone. The basal Lower Leintwardine siltstones are richly fossiliferous.

At Usk, sequences correlatable faunally with the Upper Bringewood Aymestry Limestone at Ludlow, i.e. the Lower Llanbadoc Beds (Walmsley 1959), are calcareous siltstones and nodular limestones. Despite carbonate facies influence on the fauna, Walmsley noted marked faunal differences from Ludlow, such as the absence from Usk of *K. knightii* and *Hyattidina canalis*, yet presence of *Protochonetes ludloviensis*. At the base of the overlying Upper Llanbadoc Beds, which correlate with the Lower Leintwardine Formation, a local conglomerate is followed by calcareous siltstone facies with an abundance of *D. navicula* (Walmsley 1959).

Base of Upper Leintwardine Formation

The Upper Leintwardine fauna has a number of diagnostic fossils common only in these beds, e.g. *Neobeyrichia lauensis*, *Calymene puellaris*, and *Encrinurus stubblefieldi*. Also notable are *Shaleria ornatella* and *Aegiria grayi* (Holland *et al.* 1963). The stratotype at Ludlow (SO 5071 7428) represents an intermediate sequence between two distinctive faunal units, the *S. ornatella* horizon of shelf inliers and the *A. grayi–N. lauensis* fauna of offshore shelf to trough areas. At the stratotype, the lower part of the *S. ornatella* acme is within the Lower Leintwardine Formation, and neobeyrichiid ostracodes have not been found. In other Ludlow sections these ostracodes appear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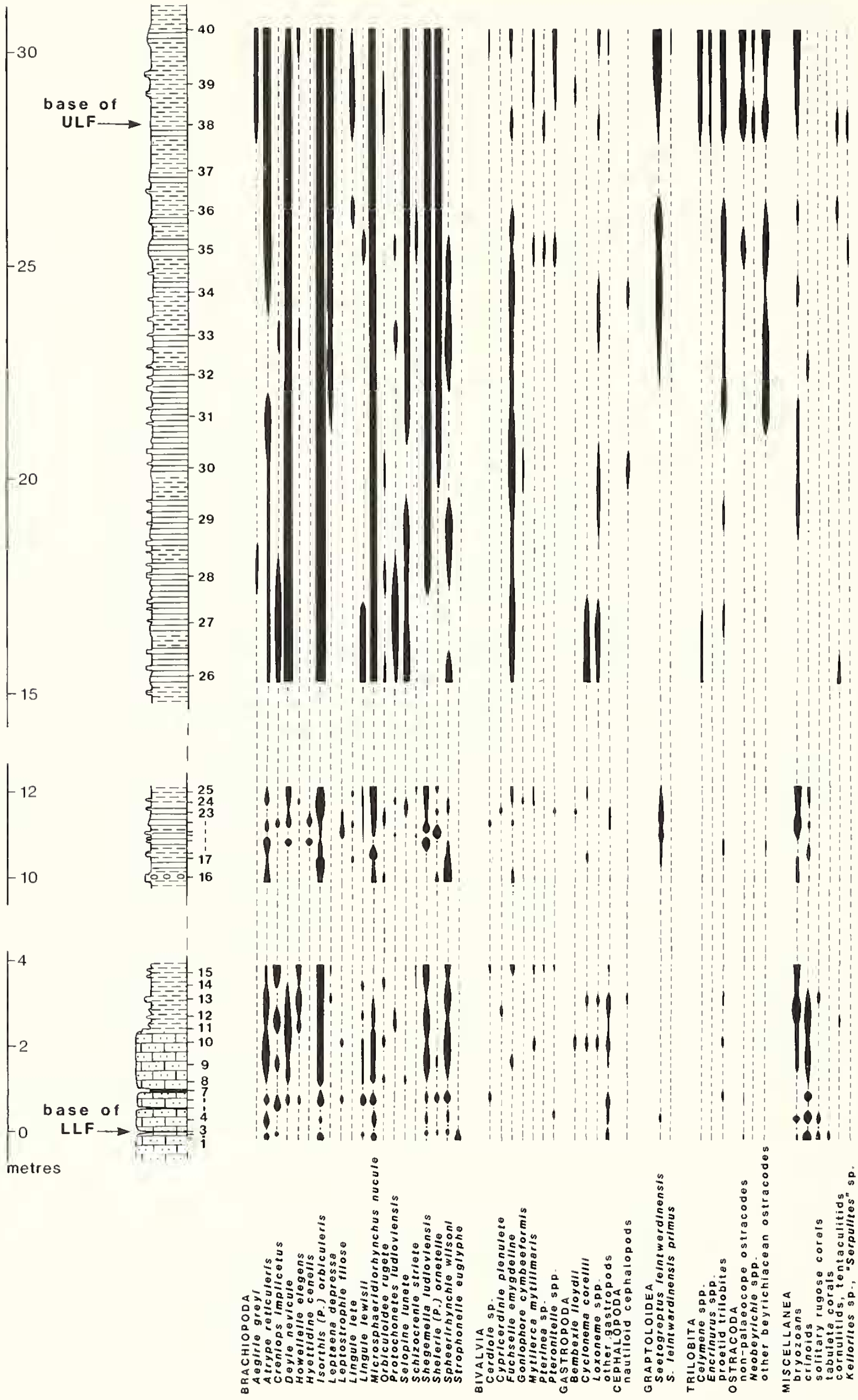
BRACHIOPODS
Aegiria grayi
Atrypa reticularis
Craniops implicatus
Dayia navicula
Howellella elegans
Hyattidina canalis
Isorthis (P.) orbicularis
Leptaena depressa
Leptostrophia filosa
Lingula lata
Lingula lewisii
Microsphaeridiorhynchus nucula
Orbiculoidea rugata
Protochonetes ludloviensis
Salopina lunata
Schizocrania striata
Shagamella ludloviensis
Shaleria (P.) ornatella
Sphaerirhynchia wilsoni
Strophonella euglypha
BIVALVIA
Cardiola sp
Cypricardinia planulata
Fuchsella amygdalina
Goniophora cymbaeformis
Mytilarca mytilimeris
Pterinea sp
Pteronitella spp
GASTROPODS
Bembexia lloydii
Cyclonema corallii
Loxonema spp
other gastropods
CEPHALOPODS
nautiloid cephalopods
GRAPTOLOIDEA
Saetograptus leintwardinensis
S. leintwardinensis primus
TRILOBITA
Calymene spp
Encrinurus spp
proetid trilobites
OSTRACODA
non-palaeocopa ostracodes
Neobeyrichia spp
other beyrichiacean ostracodes
MISCELLANEA
bryozoans
crinoids
solitary rugose corals
tabulate corals
cornulitids, tentaculites
Keilorites sp., "Serpulites" sp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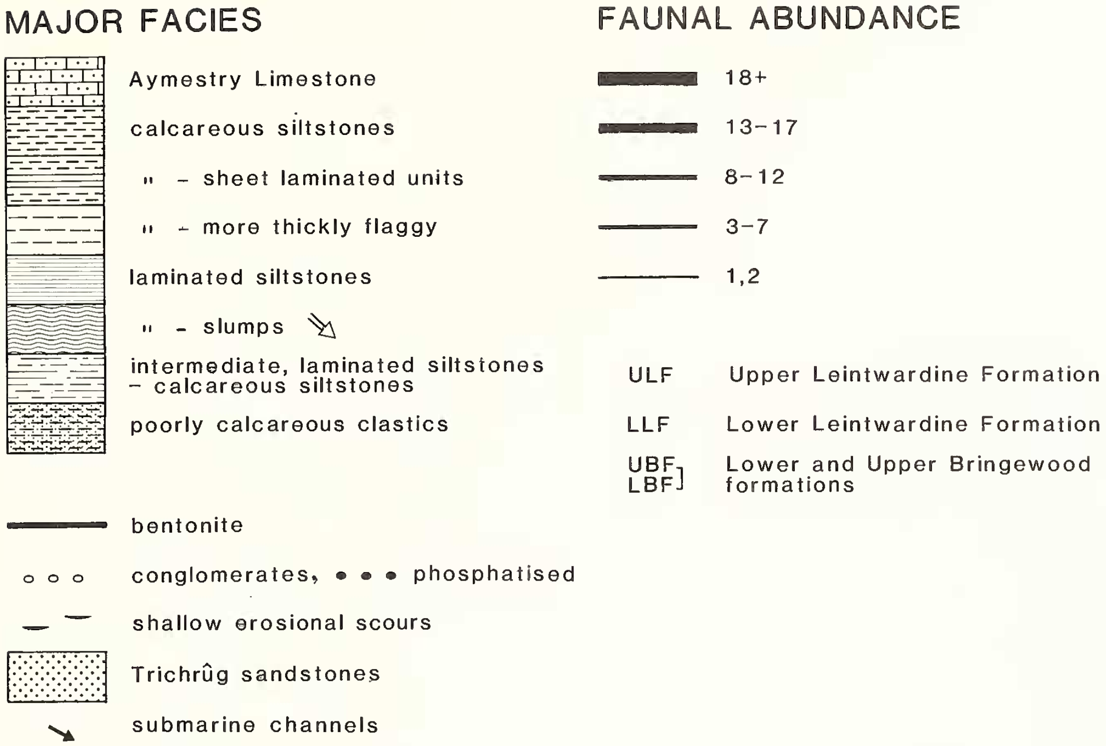
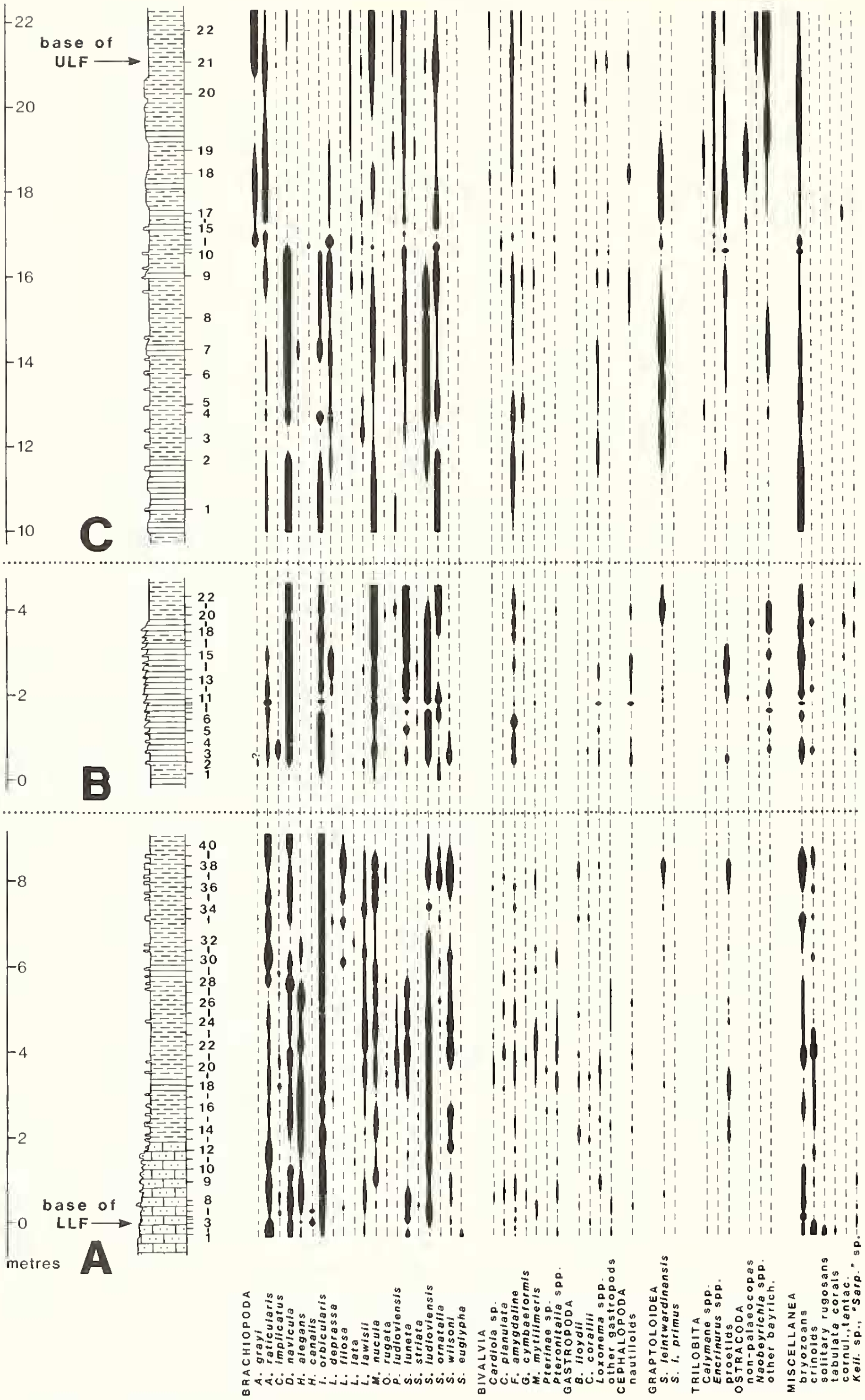
BRACHIOPODA
Aegiria grayi
Atrypa reticularis
Craniops implicatus
Dayia navicula
Howellella elegans
Hyattidina canalis
Isorthis (P.) orbicularis
Leptaena depressa
Leptostrophia filosa
Lingula lata
Lingula lewisii
Microsphaeridiorhynchus nucula
Orbiculoidea rugata
Protochonetes ludloviensis
Salopina lunata
Schizocrania striata
Shagamella ludloviensis
Shaleria (P.) ornatella
Sphaerirhynchia wilsoni
Strophonella euglypha
BIVALVIA
Cardiola sp.
Cypricardinia planulata
Fuchsella amygdalina
Goniophora cymbaeformis
Mytilarca mytilimeris
Pterinea sp.
Pteronitella spp.
GASTROPODA
Bembexia lloydii
Cyclonema corallii
Loxonema spp.
other gastropods
CEPHALOPODA
nautiloid cephalopods
GRAPTOLOIDEA
Saetograptus leintwardinensis
S. leintwardinensis primus
TRILOBITA
Calymene spp.
Encrinurus spp.
proetid trilobites
OSTRACODA
non-palaeocope ostracodes
Neobeyrichia spp.
other beyrichiacean ostracodes
MISCELLANEA
bryozoans
crinoids
solitary rugose corals
tabulate corals
cornulitids, tentaculitids
Kellorites sp., "Serpulites" sp.



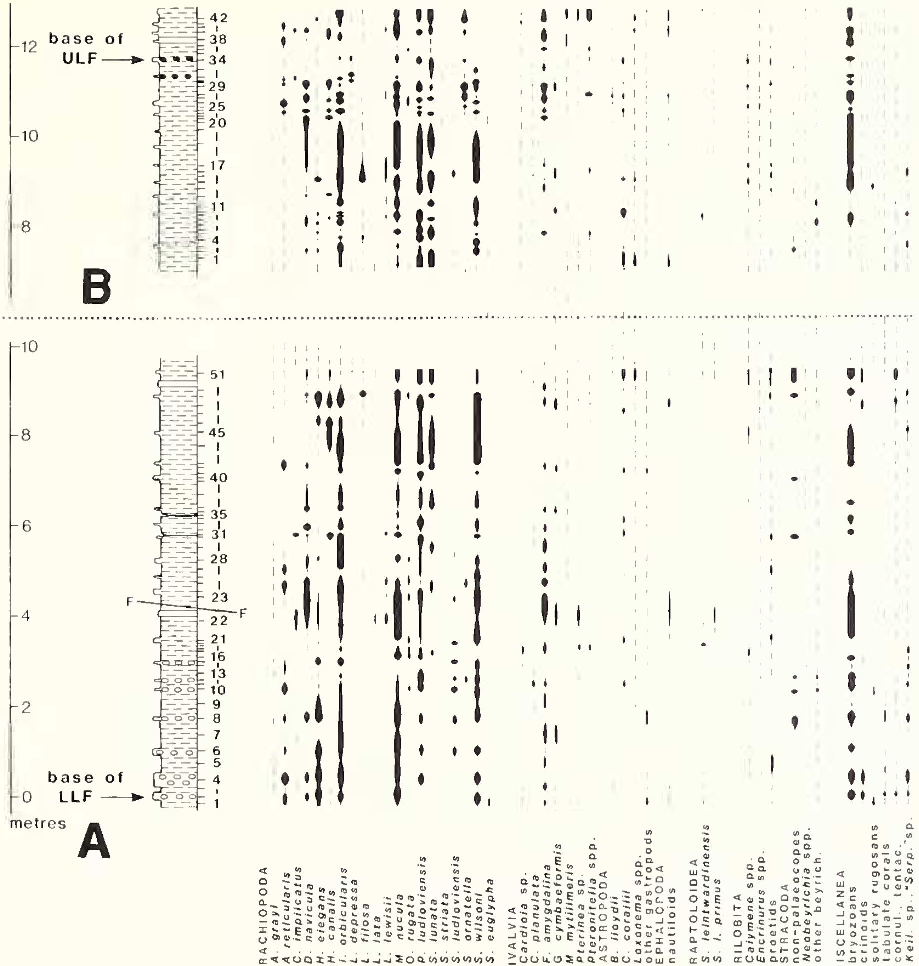
TEXT-FIG. 5. The stratigraphical range charts on text-figs. 5–12 show the major facies types and faunal abundance (for the main fauna); records for ostracodes (strictly, meiofauna) are included despite the less reliable quality of these data (see text); sample levels and numbers are shown, and positions of formation boundaries are indicated; this key refers to all range charts and palaeogeographical maps (text-figs. 5–14). Ludlow (eastern part), Sunnyhill (SO 4953 7255–4971 7246), including stratotype for the base of the Lower Leintwardine Formation.

some way above the base of the *S. ornatella* acme; e.g. in text-fig. 5 this level corresponds to the *A. grayi*-trilobite horizon, but in text-fig. 6C it is well above where *A. grayi* comes in and also above the first occurrence of *C. puellaris* and *E. stubblefieldi*. Comparable divergence of the *A. grayi*, trilobite, and *N. lauensis–N. scissa* horizons is more evident in westerly, shelf edge sequences, which lack a *S. ornatella* fauna and where a lower, *N. nutans* horizon (Siveter 1978) is also found (text-fig. 11C). Hence, since the characteristic horizon on a wider scale is the *A. grayi–N. lauensis* association, the addition of the ostracode assemblage has been taken, where possible, to indicate the base of the Upper Leintwardine Formation (cf. Shergold and Shirley 1968: = 'higher Upper Leintwardine Beds').

In the shelf inliers *A. grayi* and *N. lauensis* are rare, and known only from a few specimens at one locality at May Hill (Lawson and Whitaker 1969), *A. grayi* recorded questionably at Woolhope (Squirrell and Tucker 1960), *N. lauensis* from the Malverns (Phipps and Reeve 1967). *N. nutans* was found at Chances Pitch. Apart from this last record which is from Lower Leintwardine beds, all the others come from the thin divisions which encompass the *S. ornatella* acme. Where diagnostic trilobites are found it is mainly at this same level, except for an earlier appearance of *C. puellaris* at May Hill (text-fig. 7; Lawson (1955) took this index to mark the base of the Lower Longhope Beds) and at Chances Pitch (text-fig. 8). As at Ludlow there is no lithological change



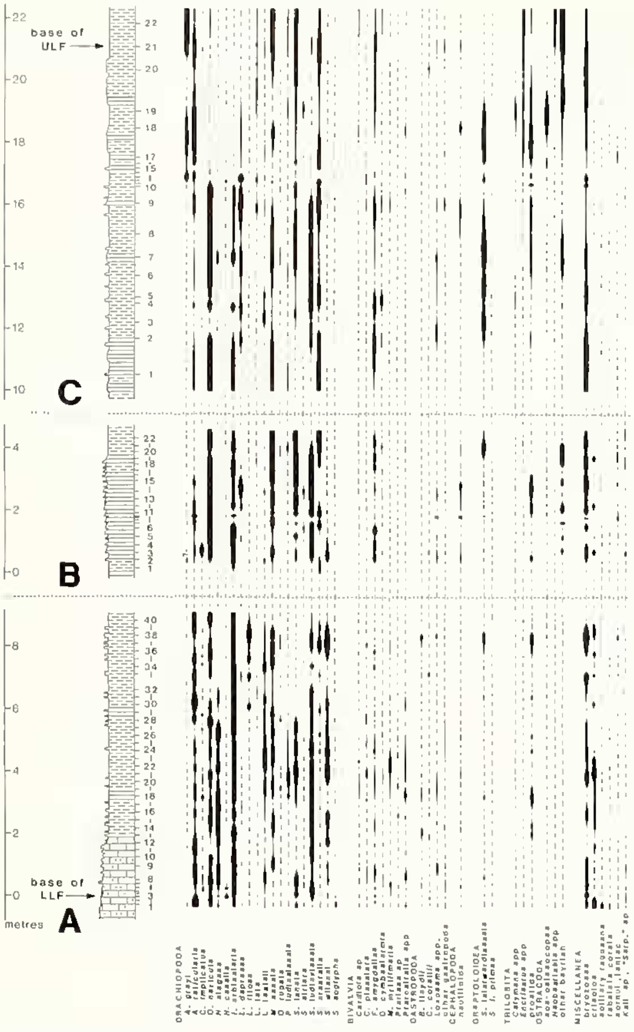
TEXT-FIG. 6. Ludlow (western part). A, lower part of succession (SO 4561 7354, 4618 7537, and 4620 7363); B, middle Lower Leintwardine Formation (SO 4893 7245); C, Haye Park, upper part of succession (SO 4876 7117–4883 7115). See text-fig. 5 description and key.



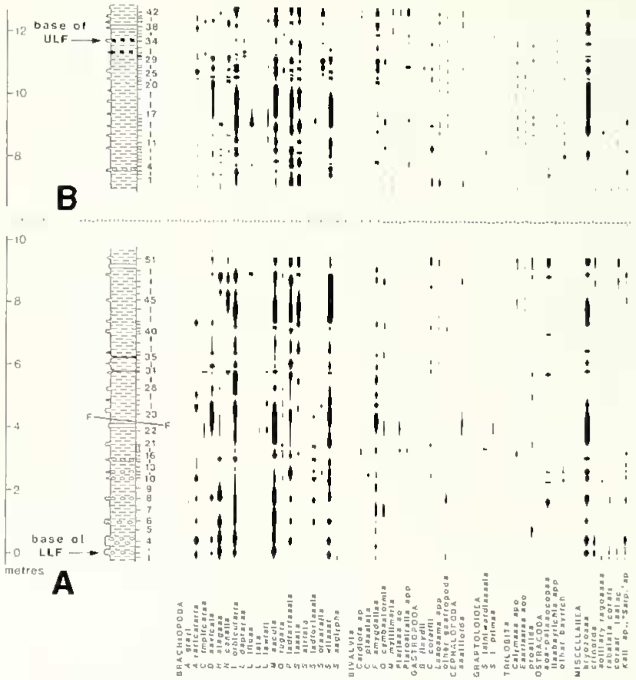
TEXT-FIG. 7. May Hill. A, Wood Green (SO 6945 1665 and 6943 1672); B, Longhope (SO 6935 1854–6939 1850). See text-fig. 5 description and key.

at the base of the Upper Leintwardine Formation in the shelf inliers. However, thin, phosphatic and conglomeratic horizons occur at several localities at around this level (p. 461).

The *S. ornatella* horizon, in its major development across the shelf region, has a rich and distinctive Upper Leintwardine Formation fauna (Holland *et al.* 1963). By contrast to Ludlow, at Woodbury and Perton the trilobite and *S. ornatella* horizons correspond to the rapid decline of *Sphaerirhynchia wilsoni*, while at Chances Pitch and Longhope the appearance of *C. puellaris* is below these changes in brachiopod emphasis (text-figs. 7–10). Also, the gap at Ludlow between the loss of *S. wilsoni* and first appearance of *N. lauensis* contrasts with a record of the two together in the Malverns (Lawson and Whitaker 1969). The base of the Upper Leintwardine Formation in shelf inliers has been taken at the level where *Shaleria ornatella* becomes abundant but also *Sphaerirhynchia wilsoni* declines rapidly: where these two overlap (e.g. at May Hill), the boundary was placed at the latter, marked faunal change.



TEXT-FIG. 6. Ludlow (western part). A, lower part of succession (SO 4561 7354, 4618 7537, and 4620 7363); B, middle Lower Leintwardine Formation (SO 4893 7245); C, Haye Park, upper part of succession (SO 4876 7117–4883 7115). See text-fig. 5 description and key.



TEXT-FIG. 7. May Hill. A, Wood Green (SO 6945 1665 and 6943 1672); B, Longhope (SO 6935 1854–6939 1850). See text-fig. 5 description and key.

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FAUNAL COMPOSITION

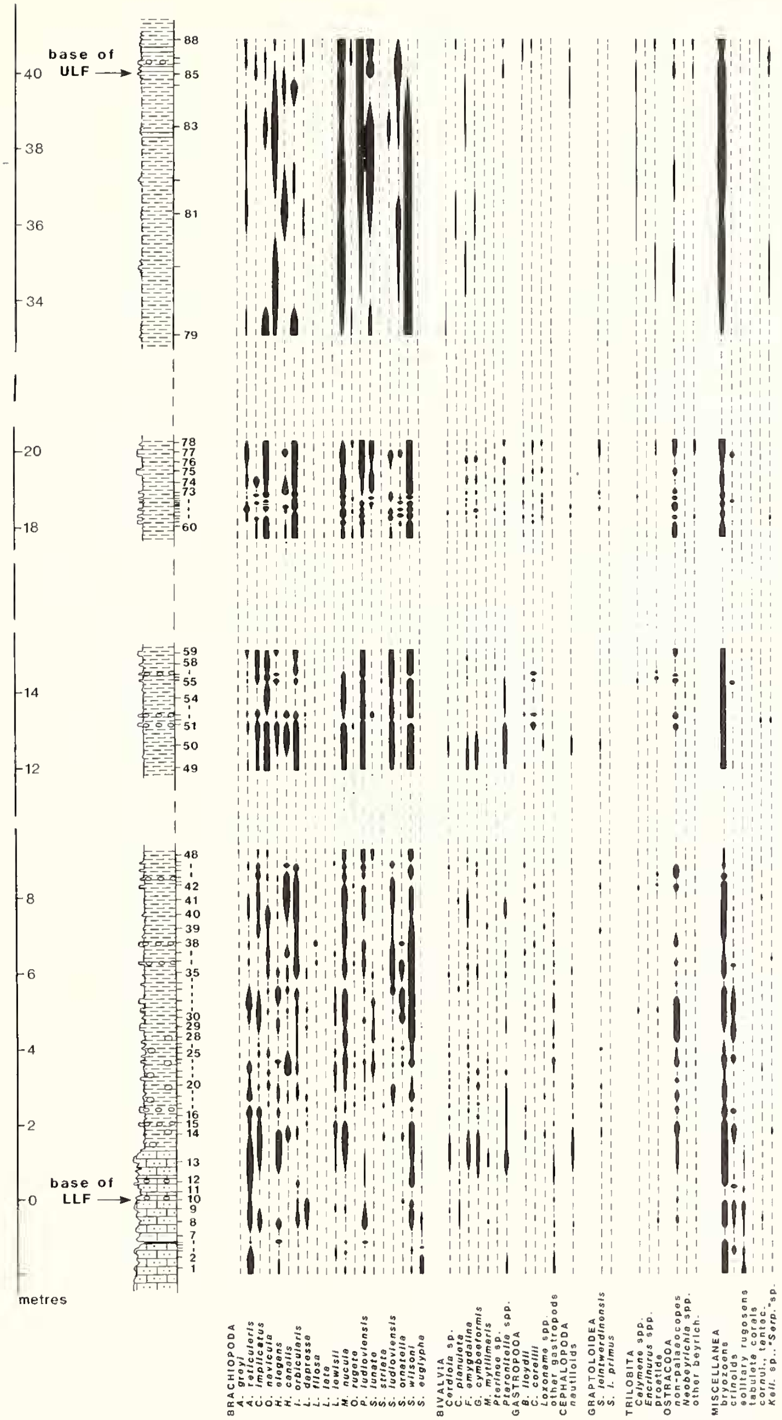
The numerous Lower Leintwardine skeletal assemblages in the calcareous siltstone facies and the top part of the Aymestry Limestone are characteristically dominated by benthic epifauna, usually articulate brachiopods (commonly $> 80\%$ of macrofauna). By contrast, in the laminated siltstone facies, benthic skeletal faunas are sparse except in intermediate, shelf edge areas and in slumped beds, and in trough sequences they are widely represented only by endofaunal inarticulate brachiopods.

The morphological adaptations of Silurian brachiopods, all of which were sessile suspension feeders, appear to relate chiefly to life attitude on or within the sediment, and to the nature of the substrate, or in broad terms to hard (rocky) or soft (level) bottom environments. All brachiopods are anchored in the juvenile, post-larval stages, the majority by pedicle attachment, and they then require hard or firm substrates. Unlike Recent brachiopods, of which the most common forms remain attached to hard bottoms throughout life, many Silurian groups changed life habit through ontogeny and became able to live on soft substrates, i.e. they were 'ambitopic' (Jaanusson 1979; 'liberosessile' of Bassett 1984). In composition early Palaeozoic benthic faunas do not demonstrate the clear distinction found in Recent seas between hard- and soft-bottom environments, where there is little ecological interaction. More varied modes of life, by comparison with Recent stocks, account for the great range of shell morphologies and sculptures in Silurian brachiopods.

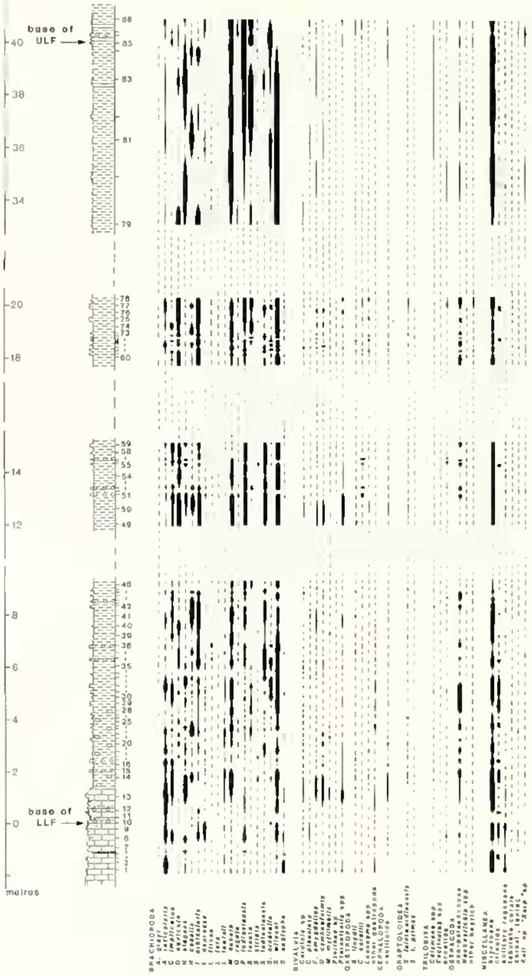
Most epifaunal species which retain an open pedicle foramen throughout life are assumed to have been pedunculate as adults ('fixosessile' of Bassett 1984). Of the common Lower Leintwardine Formation articulate species this includes the enteletaceans *I. orbicularis* and *Salopina lunata*, the rhynchonellacean *M. nucula*, and some spiriferaceans, e.g. *Howellella elegans* and *Hyattidina canalis*. These brachiopods are usually considered as hard-bottom fauna, although hard substrates for pedicle anchorage need not necessarily be more extensive than local hard patches within otherwise soft sediment, e.g. pebbles, skeletal grains. Also, the pedicle in some attached groups may have functioned largely as a tether for recumbent shells on either hard or soft substrates (e.g. Westbroek *et al.* 1975). Among populations of pedunculate brachiopods, the post-mortem detachment of shells from the substrate might provide adequate numbers of local attachment surfaces for continuing settlement of spat, although clearly such loose grains will be susceptible to current transport.

Among inarticulates, *O. rugata* and *Schizocrania striata*, which have a marginal pedicle notch on flat or slightly concave pedicle valves, represent attached, hard-bottom forms. Records of these discinaceans from upper Ludlow rocks indicate that some individuals adopted an encrusting habit on other shells, some possibly during the life of the host (Holland 1971; Lockley and Antia 1980). The shells are moulded closely to the substrate and were presumably held in place by the pedicle (cf. Recent *Discinisca*: Rudwick 1965). A few Lower Leintwardine Formation individuals of *S. striata* were found attached to larger skeletal grains, but at the only locality where this species occurs in abundance (at Aymestrey; text-fig. 11A), the numerous small, thin valves occurred separately in bedding plane assemblages, detached from their original substrates.

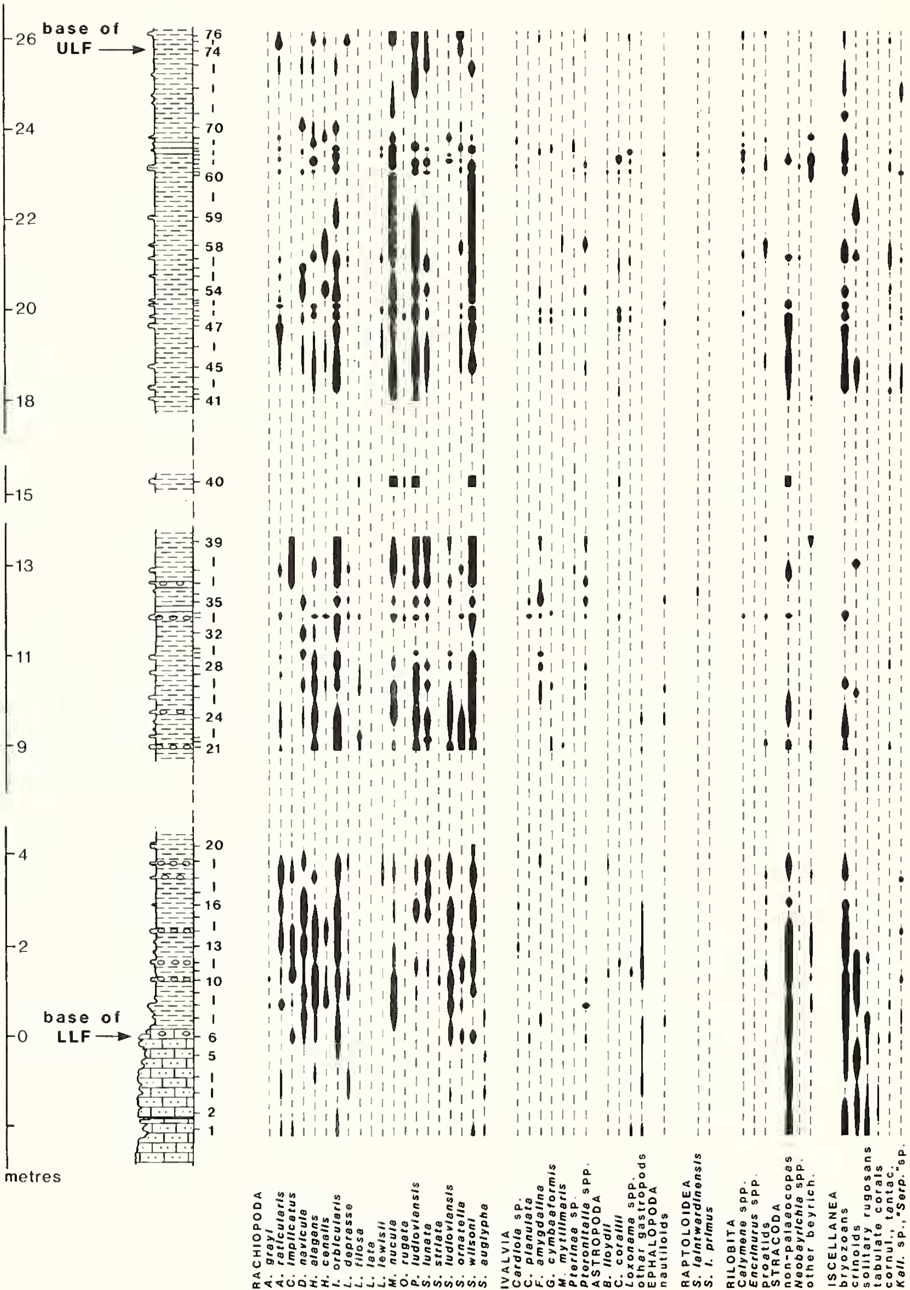
Many common Silurian brachiopods were ambitopic. The pedicle opening present in younger stages closed during ontogeny and the adults rested free (recumbent) on the sediment, as soft-bottom fauna. The free-living adults show various morphological adaptations for maintaining stability on, or partially embedded in ('quasi-infaunal' of Bassett 1984), the sediment; the latter habit can grade towards an endofaunal existence. In concavo-convex chonetaceans such as *P. ludloviensis* and *Shagamella ludloviensis*, the pedicle was lost early in ontogeny. Oblique hinge spines on the convex pedicle valve may have functioned as stabilizers (perhaps also attached distally by mucal secretion from the spine tips: Bassett 1984) in an orientation resting on that valve, possibly partially buried but with the commissure and growing mantle edges raised off the sediment. They may have been able to adjust the orientation by vigorous 'snapping' of the valves (e.g. Rudwick 1970). Strophomenaceans commonly became detached and recumbent in later stages; stropheodontides such as *Shaleria ornatella* and *Leptostrophia filosa* had relatively thin, broad,



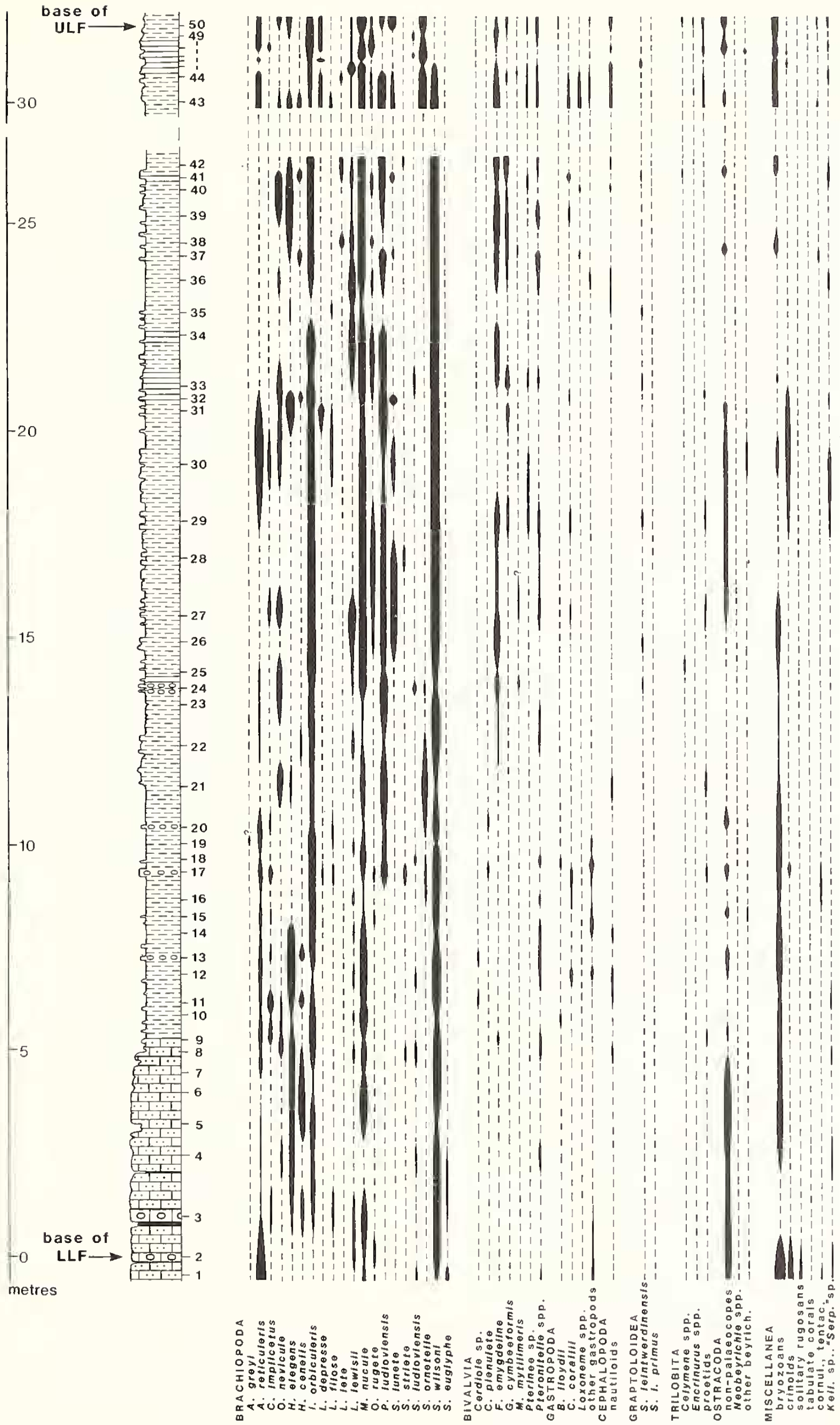
TEXT-FIG. 8. Chances Pitch (SO 7473 4018–7498 4020). See text-fig. 5 description and key.



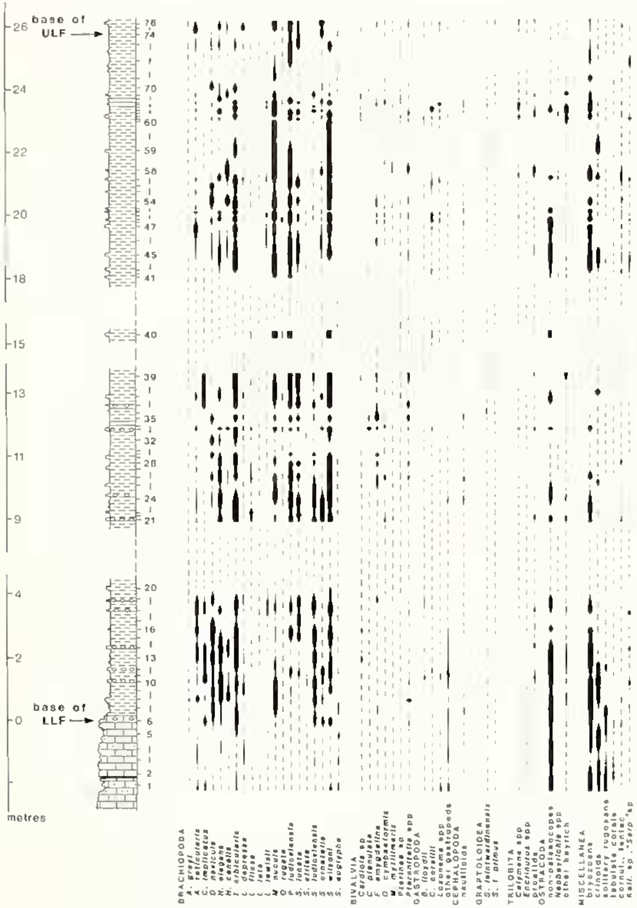
TEXT-FIG. 8. Chances Pitch (SO 7473 4018–7498 4020). See text-fig. 5 description and key.



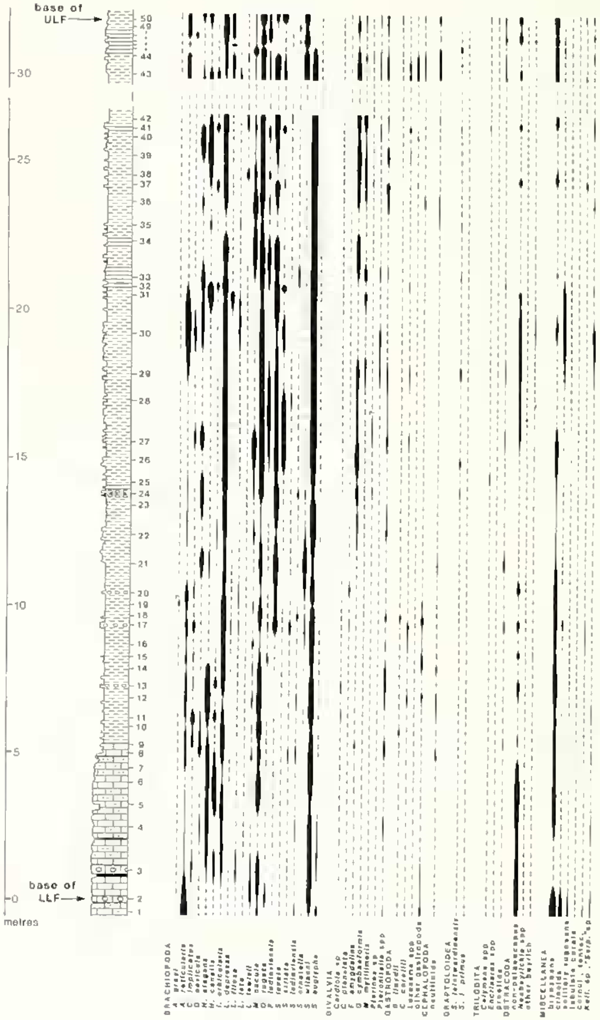
TEXT-FIG. 9. Perton (SO 5952 3995 and 5963 4012). See text-fig. 5 description and key.



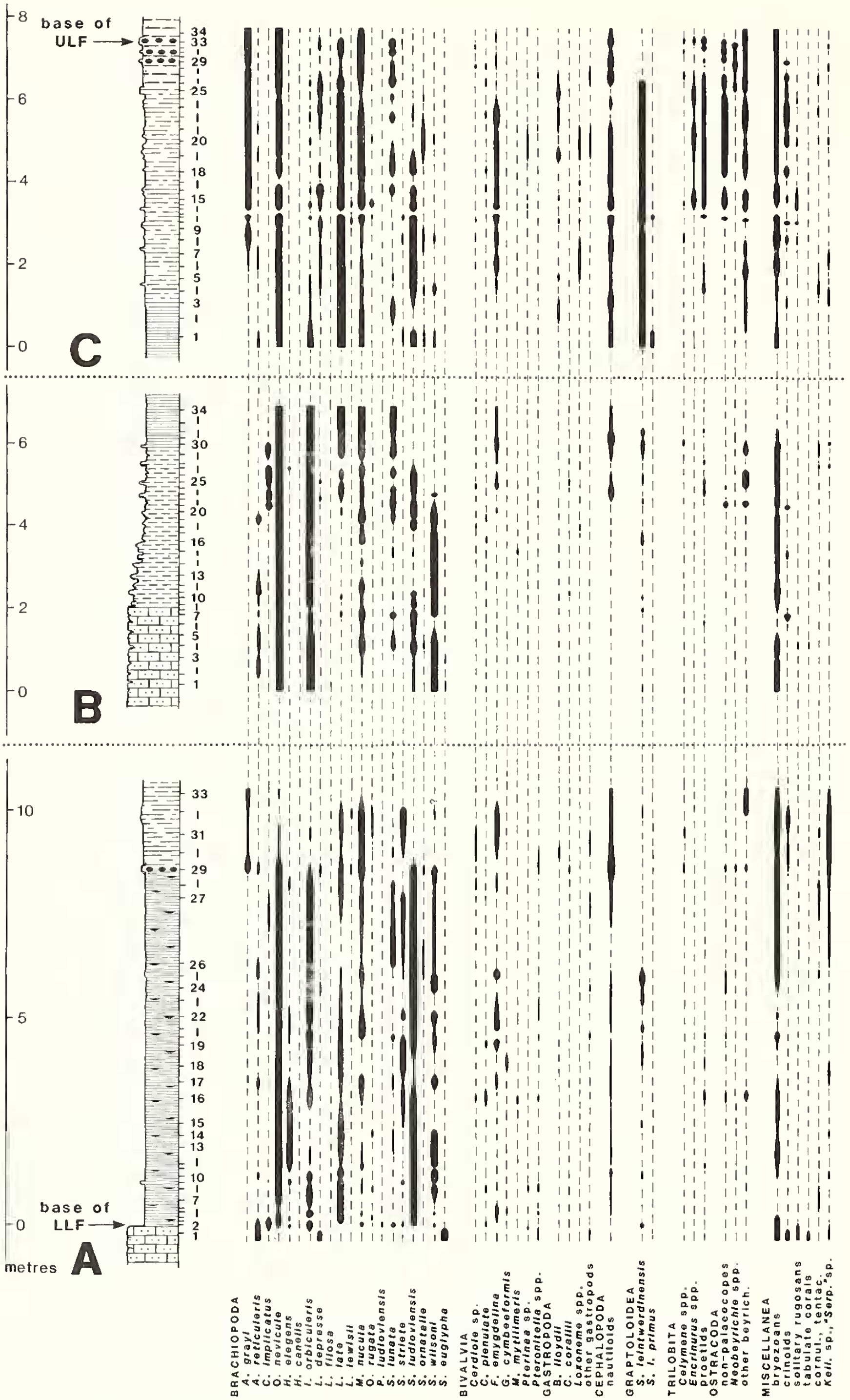
TEXT-FIG. 10. Woodbury (SO 7430 6368). See text-fig. 5 description and key.



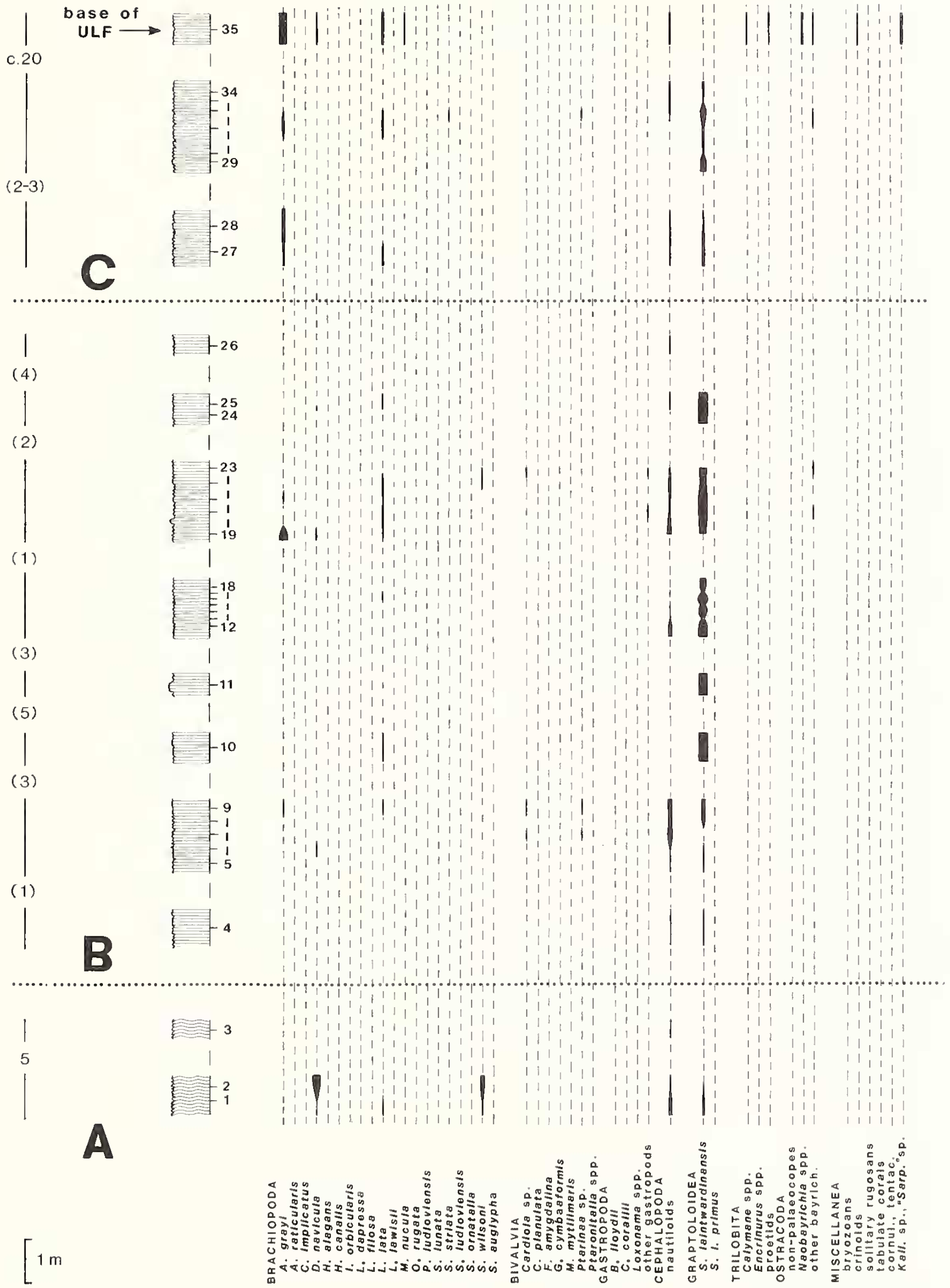
TEXT-FIG. 9. Perton (SO 5952 3995 and 5963 4012). See text-fig. 5 description and key.



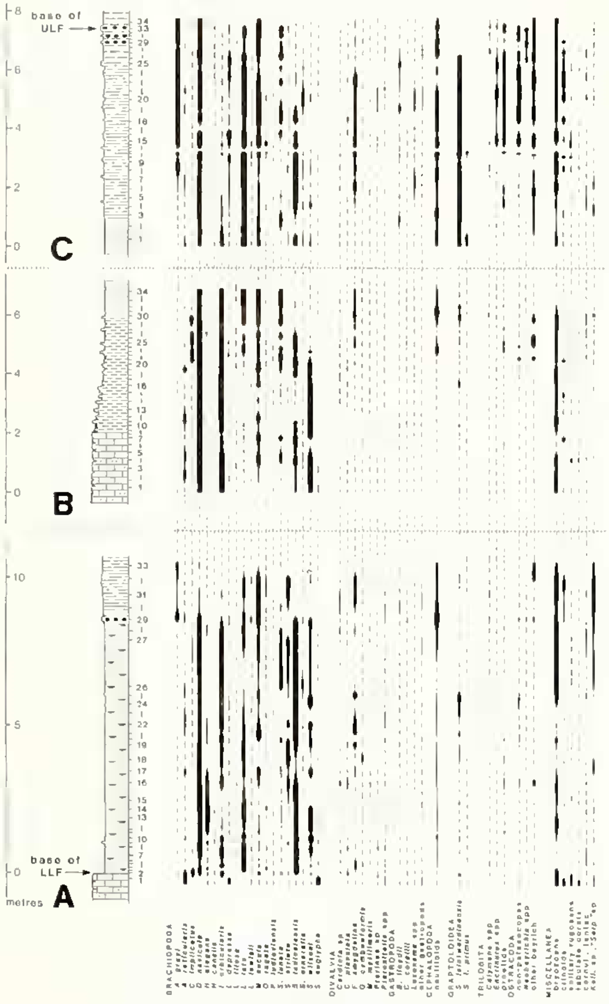
TEXT-FIG. 10. Woodbury (SO 7430 6368). See text-fig. 5 description and key.



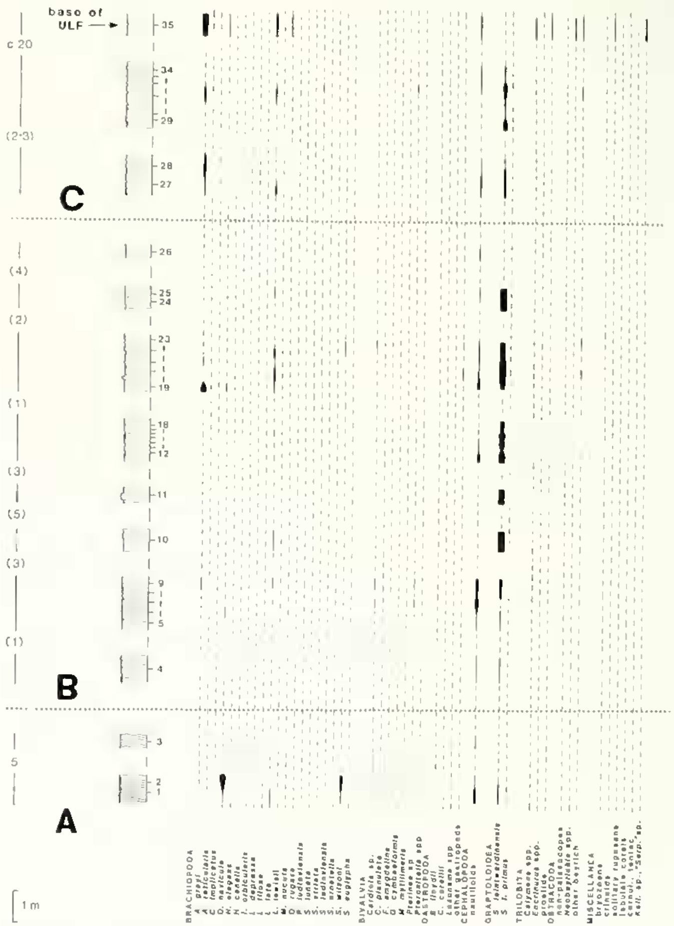
TEXT-FIG. 11. Aymestrey and Leintwardine. A, Aymestrey (SO 4220 6546); B, Lawnwell Dingle, succession from *c*. 1–2 m above base of Lower Leintwardine Formation (SO 4163 7677); C, Shelderton (SO 4172 7790–4178 7792). See text-fig. 5 description and key.



TEXT-FIG. 12. Kerry. A, Ring Hole gorge, upper part of slump sequence (SO 1242 8365); B, Pant-y-llidiart lane to Cwm, upper part of *M. leintwardinensis* Shales (SO 1615 8747–1630 8743); C, Pant-y-llidiart dingle, upper part of *M. leintwardinensis* Shales (SO 1650 8770–1647 8735). Approx. gaps (m) between sample points shown in parentheses. See text-fig. 5 description and key.



TEXT-FIG. 11. Aymestrey and Leintwardine. A, Aymestrey (SO 4220 6546). B, Lawnwell Dingle, succession from *c*. 1-2 m above base of Lower Leintwardine Formation (SO 4163 7677); C, Shelderton (SO 4172 7790-4178 7792). See text-fig. 5 description and key.



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gently concavo–convex shells where the large surface area would provide support on the sediment surface. In *Leptaena depressa*, the wide geniculate adult shell with a pronounced fold and trail may represent adaptation to a quasi-infaunal habit where the commissure remained free of the substrate even though the shell was largely buried (e.g. Rudwick 1961; Bassett 1984). Among the common Upper Bringewood Formation forms, *Strophonella euglypha* and *Amphistrophia funiculata* show similar morphological adaptation, with geniculate adult shells.

Adult forms of the biconvex athyridacean *Dayia navicula* and the atrypacean *Atrypa reticularis* show marked secondary thickening of the umbo region in the pedicle valve, while incurvature of the beak area and sealing by plate structures during growth resulted in reduction or loss of the pedicle opening (e.g. Tucker 1964). The distribution of these species suggests that a clustered, gregarious life habit was a common, though not invariable, feature of populations. Stability was maintained partly by embedding of the posteriorly weighted shell in the sediment, but additionally by close juxtaposition with neighbouring individuals; this strategy was termed 'co-supportive' by Bassett (1984). Worsley and Broadhurst (1975) described clustered populations of *A. reticularis* in the Llandovery of the Oslo region, for which loss of the pedicle varied among individuals but where most larger, adult shells were detached, resting on the flatter pedicle valve with its broad fringe or supported by adjacent shells. Many Silurian pentameraceans display this type of occurrence in fairly high energy environments, e.g. *Pentamerus oblongus* and *Stricklandia lens* in the Llandovery (Ziegler *et al.* 1966), and *K. knightii* in the high energy carbonate facies of the Upper Bringewood Formation.

A comparable strategy may have applied also to close packed populations of some rhynchonellaceans (e.g. *Sphaerirhynchia wilsoni*) to supplement the anchoring function of the pedicle. Although the shell is not thickened posteriorly, there was umbonal incurvature resulting in reduction or loss of the pedicle. In *S. wilsoni* an umbo-down posture was apparently maintained by increased globosity and geniculation, the adults adopting a quasi-infaunal habit partially buried in the sediment (Westbroek *et al.* 1975; Fürsich and Hurst 1981).

The small ambitopic inarticulate lingulacean *Craniops implicatus* has a cicatrix for direct attachment to a hard grain in early ontogeny. It became detached still at a relatively young stage but at a size that allowed independent stability. The adult has a limbus which would tend to stabilize the recumbent shell (e.g. Bassett 1984).

In general, the distribution of both hard- and soft-bottom brachiopods in the Leintwardine formations shows a marked concentration to shelf areas (text-figs. 5–12). However, the small, thin-shelled plectambonitacean *Aegiria grayi*, which has a narrow pedicle foramen and was probably pedically attached (Cocks 1970), has a distribution notable for its concentration in western, outer shelf areas. Its occurrence there is commonly among restricted assemblages, in association with ostracodes but largely separate from assemblages of other epifaunal brachiopods. The small, light concavo–convex shell, which is similar morphologically to the recumbent to quasi-infaunal chonetaceans and strophomenaceans, has been discussed variously as an adaptation to low-energy offshore, soft-bottom conditions or to an epiplanktic mode of life attached to floating algae (cf. *Sargassum*, e.g. Fürsich and Hurst 1974; Watkins and Berry 1977). An epiplanktic habit has been proposed for several Ordovician and Silurian articulate brachiopod genera with similar general morphology, mostly to explain their occurrence in offshore, graptolitic shales, e.g. *Sericoidea* (Bergström 1968), *Chonetoidea* (Havlìček and Vaněk 1966; Havlìček 1967), *Aegiria* and *Shagamella* (Watkins and Berry 1977). Except apparently for *Aegiria*, these brachiopods lost a functional pedicle during ontogeny and thus lacked the means of attachment to an algal or other floating substrate (unless the short hinge spines of *Shagamella* could achieve this: Bergström 1968). For unattached forms an epiplanktic habit would seem unlikely, and it is notable that some Recent benthic brachiopods inhabit zones down to abyssal depths (e.g. *Pelagodiscus*: Rudwick 1970). Cocks (1970) noted the main Llandovery distribution for *Aegiria* as being in the 'deepest' benthic, *Clorinda* community, but suggested that occurrences in trough sequences where benthic fauna was otherwise scarce might be explained by offshore transport along with an uprooted algal substrate. Sheehan (1977) proposed alternatively that fallen seaweed might provide patches of relatively firm substrate for benthic organisms in offshore areas of soft sediment. For *A. grayi* in the Lower and Upper Leintwardine formations, a pedunculate, possibly recumbent benthic habit in offshore environments explains its distribution, yet an epiplanktic life-style cannot be discounted. However, for the heavier shelled, ambitopic *S. ludloviensis*, which is concentrated among benthic shelf assemblages, a benthic life habit seems probable (cf. Watkins 1979, for Lower Bringewood Formation).

Of the benthic fauna associated with brachiopods across the shelf, bivalves form minor components of many skeletal assemblages and are even prevalent locally, although not generally in comparable numbers with brachiopod dominated assemblages. Except for pterineids, bivalves also are concentrated mainly on the shelf. All the more common Lower Leintwardine Formation bivalves represent suspension-feeding benthos. Most were byssally attached, either endobyssate, i.e. partly buried in soft sediment, e.g. *Cypricardinia*, *Goniophora*, *Pteronitella*, or epibyssate on hard substrates, e.g. *Mytilarca*, *Pterinea* (e.g. Stanley 1972). The most common bivalve, *Fuchsella*, may have been a slow, shallow burrower since it lacks a byssal sinus or gape; otherwise it was probably endobyssate.

Bryozoans occur widely in shelf sequences, but their usual fragmentation among skeletal assemblages means that diversity may be underestimated. They are hard-bottom, suspension feeding epifauna, and most require firm though not necessarily large attachment sites (e.g. Brood 1979, 1984). In the Lower Leintwardine Formation ramose forms appear best represented, although the bifoliate cryptostome *Ptilodictya lanceolata* is conspicuous in shelly conglomerates. Most bryozoans are dissociated from their original substrates. Encrusting and fenestellate forms are however found on some skeletal grains, most prominently on abraded fossils in phosphatized horizons of high Lower Leintwardine–Upper Leintwardine Formation beds.

Crinoids and solitary corals are further attached, suspension feeding organisms that form minor parts of hard-bottom epifaunas. Like bryozoans, they may have required only local hard sites for attachment; a few corals are attached to a skeletal fragment, but crinoids are dissociated from their original substrates and largely disaggregated. Both these groups are considerably less abundant than in the underlying Upper Bringewood Formation.

The hard-bottom endofauna is generally poorly represented in early Palaeozoic benthic faunas by comparison with Mesozoic and Recent examples (e.g. Palmer 1982). The only evidence of this group in the Lower Leintwardine Formation is from small borings (*Trypanites*) which affect clasts in conglomerates, and from a few small circular bored cavities on skeletal grains. The low density of these organisms suggests that their activity was unimportant as a destructive factor on hard substrates.

Apart from quasi-infaunal brachiopods and endobyssate bivalves, the endofauna of soft substrates is represented in skeletal assemblages chiefly by lingulide brachiopods. Both the common Lower Leintwardine Formation species *Lingula lewisii* and *L. lata* appear, from the not uncommon occurrence of individuals perpendicular to the bedding and thus apparently *in situ* (Cherns 1979), to have been burrowers like Recent *Glottidia* and *Lingula* (e.g. Thayer and Steele-Petrovic 1975; Emig 1982; Hammond 1983). The very different distribution patterns for the species appear to result from different palaeoecological tolerances, comparable to the range known from Recent environments (e.g. Emig *et al.* 1978; Plaziat *et al.* 1978), and not as Watkins and Berry (1977) suggested to adoption of an aberrant, epiplanktic existence by *L. lata* (Cherns 1979). *L. lata* typically represents the only benthic skeletal fauna through much of the laminated siltstone facies in trough areas.

Other endofaunal or semi-endofaunal skeletal organisms which occur in very minor numbers are tentaculitids and cornulitids (e.g. Larsson 1979), and tube-dwelling worms such as '*Serpulites*' *longissimus* and *Keilorites* (e.g. Brood 1979). However, endofaunal activity is indicated throughout the shelf by commonly intense bioturbation of sediments, caused by vagile benthos of which the major proportion was probably soft-bodied organisms, as in Recent environments (e.g. Craig and Jones 1966). By contrast to the sessile benthos, this sediment-reworking vagile benthos represents mainly deposit feeders. In the trough sequences of the laminated siltstone facies, the scarcity or absence of bioturbation traces indicates that conditions were inimical to endofaunal deposit feeders.

The vagile benthos, which is less restricted by substrate or habitat than sessile organisms, comprised mainly arthropods and molluscs. Quantitatively, this faunal component is poorly represented through much of the Lower Leintwardine Formation. Of the trilobites, some calymenids were apparently capable of burrowing (e.g. Osgood 1970) and encrinurids may, like some cybelines (Ingham 1968), have been able to conceal themselves in the sediment. However, it is probable that all also spent part of the time actively searching for food, whether as deposit feeders, hunters, or scavengers. Eurypterids, as active predators, were probably similarly epifaunal, crawling or swimming but also able to burrow or hide temporarily within the sediment. Ostracodes, which in size belong to the small macrofauna or meiofauna, include both palaeocope and non-palaeocope groups; beyrichiid ostracodes were apparently benthic, but it is uncertain to what extent they lived in or on the sediment or associated with algal vegetation (e.g. Siveter 1984). Of the vagile molluscs, early Palaeozoic archaeogastropods, which occur only in minor numbers, are thought chiefly to represent epifaunal deposit-feeding microherbivores or algal browsers. Some forms, e.g. bellerophontids, were apparently adapted to soft substrata, by contrast to most Recent representatives of this order (e.g. Peel and Wängberg-Eriksson 1979). Orthocone and cyrtocone nautiloids are generally poorly preserved, occurring widely but in low numbers. For Silurian nautiloids, Mutvei (1979) noted the commonly small muscle attachment scars and he interpreted the functional morphology of the siphonal tube as regulatory. He suggested that many nautiloids were possibly pseudoplanktic rather than benthic, as scavengers or rather inactive predators. The chambered, buoyant shell might drift extensively after death of the animal, and nautiloids are most numerous among laminated siltstone sequences of trough areas, both dispersed and in current-aligned assemblages (Hewitt and Watkins 1980).

Graptolites, as planktic organisms, were independent of the substrate type and benthic communities. Their dominantly troughward distribution presumably reflects prevailing currents or water mass distribution, modified by preservational factors. Particularly in shelf areas the more turbulent environments were likely to destroy the fragile skeletons.

Faunal associations—palaeocommunities?

Much has been written on the composition and palaeoecological significance of recurrent benthic fossil assemblages from Lower Palaeozoic sequences. Approaches encompass various taxonomic levels, commonly with an emphasis upon articulate brachiopods as representing the major elements of faunas, although some studies have also included associations dominated by other groups, and with assemblages ranging from local to global in extent (e.g. Ziegler *et al.* 1968; Boucot 1975, 1981; Jaanusson 1979; Williams *et al.* 1981). Various interpretations have been made with regard to controls by factors such as depth, substrate, and water energy (e.g. Hancock *et al.* 1974; Hurst 1975; Lawson 1975; Noble 1979; Jaanusson 1979); a broader shoreline-related environmental classification was proposed for brachiopods by Boucot (1975). More recently the concept of depth regulation of Silurian brachiopod communities has been applied to models for regional sea-level changes (e.g. Johnson *et al.* 1981).

In referring to recurrent fossil associations as 'communities', or using ecological terms to describe them, it should be stressed that the composition of fossil assemblages bears only limited relation to any original community structure, and that the evidence from sediments for controls on species distribution is inadequate (e.g. Craig and Jones 1966). However, as the best means available for comparison of fossil with Recent faunas and ecosystems the use of such terminology has become widespread (e.g. Williams *et al.* 1981; Boucot 1981). Here, the Lower Leintwardine shelf faunas have been subdivided into several facies-related benthic associations, each subject to fluctuating composition in terms of diversity, density, frequency of occurrence, extent, and in the nature of the embedding sediments. Whether or not the composition of an association represents an ecological distribution depends largely upon the degree of transport and mixing of faunas involved during sediment accumulation. In addition, a thanatocoenotic association characteristic of basin sequences is described.

The faunal data derived from the main transect from shelf to basin are displayed in text-figs.

5-12. It is evident that the complexity of faunal distribution relates closely to the sampling frequency (e.g. the detailed patterns of text-fig. 7, cf. more spaced collections in the upper part of text-fig. 5). It is characteristic of individual assemblages that a single species is locally dominant, yet the prevalent species changes from bed to bed and even laterally along bedding surface layers (text-fig. 3). Analysis of skeletal distribution in shelf sequences suggests that this highly variable composition of assemblages represents an original pattern of rapid and local fluctuations in relative species abundance (p. 469). Some monospecific assemblages appear to have undergone more rigorous current reworking, but there is no indication that this has caused significant mixing of faunal 'belts' (p. 473). Comparison of statistically defined brachiopod communities for the Ludlow (Calef and Hancock 1974) with the Lower Leintwardine faunas would suggest change in 'depth-related' community from bed to bed, but no single, low diversity assemblage can be taken alone as a broader environmental index (e.g. Lawson 1975; Cherns 1979; Watkins 1979). A wider approach encompassing faunal distribution related to overall facies definition, and hence to environmental factors, presents a more representative picture of the faunas (also Watkins 1979). Thus, while there is clearly an overlap in individual species distribution, several associations can be recognized which relate broadly to position and sedimentation patterns along a shelf to trough transect, and also to stratigraphical level.

Lower Leintwardine Formation faunal associations

Within the areas of calcareous siltstone facies the different ranges occupied by individual brachiopod species were apparently a response primarily to physical stresses along environmental gradients. Within a species range, large local fluctuations in relative abundance appear to represent more temporary controlling factors, e.g. larval recruitment. In Recent environments the most marked faunal boundaries relate to changing sedimentation zones along shelf to trough profiles (e.g. Dörjes 1971; Reineck and Singh 1980). In the Lower Leintwardine Formation the greatest lateral faunal change, from dominantly shelly to graptolitic sequences, corresponds through much of the unit to the offshore edge of the calcareous siltstone facies belt. Only in the basal part of the laminated siltstone sequences of shelf edge areas (e.g. Aymestrey) were shelly faunas common, and these disappeared rapidly towards the areas of greater subsidence not far further west (e.g. Lyepole Bridge). Subdivision may be made primarily within the calcareous siltstone facies of the shelf region into three broad, subtidal benthic faunal associations dominated by epifaunal, suspension-feeding articulate brachiopods, which characterized the Leintwardine formations. A lack of distinct facies boundaries explains the transitional and intergrading composition of these associations, which describe overall changes in faunal emphasis. In general, changing faunal associations represent faunal shifts; immigrations (*sensu* Jaanusson 1979) are few, the most notable being the incoming in late Leintwardinian times of neobeyrichiid ostracode and trilobite faunas of Baltic aspect. In relation to Boucot's (1975) classification of benthic faunas these associations correspond to Benthic Assemblages 2 to 4.

The first two associations represent lateral equivalents which characterized more inshore and offshore shelf areas respectively through the major part of the Lower Leintwardine Formation. They replaced the Upper Bringewood lower energy carbonate faunas which Watkins (1979) termed the '*Atrypa reticularis*-coral Association', the high energy carbonate faunas with *Kirkidium knightii* and tabulate corals ('*K. knightii* Association': Watkins and Aithie 1980), and also the strophomenid-rich faunas of adjacent areas of silt deposition. The Lower Leintwardine sedimentary facies, which dominantly represent shelf silt environments, indicate frequent higher energy disturbances leading to accumulation mainly of epifaunal but also shallow endofaunal skeletal fossils. Marked and rapid, local faunal shifts and low diversity assemblages are concluded to relate to original patch distributions and to domination by opportunistic species. It is apparent that the carpets of shells and skeletal debris produced by episodes of scouring of surficial sediment might provide areas of 'hard' substrate, yet the relatively infrequent destruction and disturbance of skeletal beds as a result of endofaunal activity suggest that many such layers rapidly became buried by sediment, perhaps as a result of the same erosional events.

Association A. In inshore shelf sequences, and also through the top of the carbonate formation into calcareous siltstone facies in the Wenlock Edge region, the fauna concentrated into winnowed skeletal layers is dominated particularly by an abundance of the rhynchonellides *Sphaerirhynchia wilsoni* and *Microsphaeridiorhynchus nucula*, and *Isorthis orbicularis*. A number of other brachiopod species also occur in abundance and prevalently, although less widely or through more limited parts of sequences, e.g. *D. navicula*, *Howellella elegans*, *Hyattidina canalis*, *Protochonetes ludloviensis*, *Salopina lunata*, and *Shagamella ludloviensis*. These brachiopods include attached, hard substrate species, and cosupportive forms, e.g. *D. navicula*, *Sphaerirhynchia wilsoni*, but also recumbent, soft-bottom forms, such as the chonetaceans. Bryozoans and crinoids are associated hard-bottom faunas, although these smaller and fragmented skeletal grains may represent more extensively transported sand and gravel grade material. The soft-bottom, semi-endofaunal or burrowing bivalve *F. amygdalina* occurs widely and is prevalent in some bedding surface assemblages, but the main indication of local endofauna, apart from *in situ L. lewisii*, is from the commonly intense bioturbation of sediments. The same faunal association also characterizes the high energy limestone conglomerates of the lower part of the Lower Leintwardine Formation, where *in situ* hardground formation occurred widely (even within individual deposits). The bryozoan *Ptilodictya lanceolata*, which anchored by a cemented holdfast, is common in these beds, and attached, strongly ribbed, and robust shelled brachiopods are widely, though not invariably, prevalent.

Association B. In areas further out on the shelf, where sheet-laminated deposits are prominent among sequences (e.g. Ludlow, text-fig. 6B), and through the lateral transition into the basal laminated siltstone facies of the Leintwardine to Aymestrey region, a mid-shelf to offshore association is dominated by *D. navicula*, *I. orbicularis*, and *Shagamella ludloviensis*. Of these, only *I. orbicularis* was a hard-bottom form, the other two species being ambitopic and adapted as adults to a recumbent mode of life. Assemblages are commonly virtually monospecific. Other common species of the first association also occur in some abundance in the mid-shelf part of this zone (e.g. at Ludlow). However, by comparison, *Protochonetes ludloviensis* does not become common here until higher beds (cf. Lower and Upper Whitcliffe formations), and *Salopina lunata* has a more limited distribution (again more common in younger beds). *Sphaerirhynchia wilsoni* and *Howellella elegans* are chiefly common only in the lower part of the Lower Leintwardine Formation, through the carbonate-silt transition, and the former is much less prominent overall. *Hyattidina canalis* is not common. Through its main development, this association has fewer common brachiopod species. The infaunal *L. lewisii* is widely distributed and becomes locally numerous *in situ* in some beds, in what presumably represent rapidly buried assemblages among the sheet-laminated facies. The soft-bottom bivalve *F. amygdalina* dominates some assemblages. As in the first association intense bioturbation indicates the activity of soft-bottom endofauna. Currents which produced the sheet-laminated beds scoured the surface sediment, and these beds include accumulations of skeletal epifauna and shallow infauna. The similarities of sediment grade and faunal composition to interbedded sediments argue against extensive transport and faunal mixing having taken place.

Towards the shelf edge, *I. orbicularis* is found in comparable abundance only in the lowermost Lower Leintwardine beds (also, Alexander 1936). *D. navicula* occurs in enormous, monospecific abundance at the top of the higher energy carbonate facies through into the siltstones (e.g. text-fig. 11B), and *Shagamella ludloviensis* is prevalent with it in the very thinly bedded, basal laminated siltstone facies (e.g. text-fig. 11A). In the latter facies (e.g. Aymestrey), valves of the smaller infaunal lingulide *L. lata* are very common, and also of the epifaunal attached inarticulate *Schizocrania striata*? However, the two small, soft substrate species *D. navicula* and *Shagamella ludloviensis* are greatly dominant. The absence or limited traces of bioturbation in the sediments suggest a greatly reduced soft-bottom, deposit-feeding endofauna. In relation to Ludlow, the main brachiopod fauna is less diverse, and it is notable that small, smooth or finely ribbed, and thin shelled forms are more prominent. The action of offshore, shelf to trough currents is evident from, for example, the linear scour grooves at Aymestrey, and there are some thin, laminated silt sheets. Small and light valves might be relatively easily transported, yet the limited damage among derived, convex-up assemblages indicates only moderate current energy and reworking, and generally lower energy conditions prevailed in these outer shelf areas of muddy, finer grained sediment. Above the lower part of the laminated siltstone facies in these areas, skeletal faunas become relatively sparse.

Association C. The third association of the calcareous siltstone facies is the *Shaleria ornatella* fauna of the high Lower Leintwardine–Upper Leintwardine beds, which has a very wide but stratigraphically restricted distribution across the shelf region. It is characterized by marked, even monospecific abundance of this recumbent stropheodontide, widely corresponding closely to the disappearance from sequences of *Sphaerirhynchia wilsoni* and *Shagamella ludloviensis*, and to minor acmes of *Leptaena depressa* and *Atrypa reticularis*. *Salopina lunata*, *P. ludloviensis*, and *M. nucula* are also notably common at this level. Arthropods, molluscs, and bryozoans form minor faunal elements. The association is thus dominated by large, soft-bottom epifaunal to quasi-infaunal brachiopods, together with some hard substrate species. There are both epi- and endobyssate or shallow burrowing bivalves, and diverse vagile skeletal benthos. The sedimentary facies indicate similar physical conditions to beds below, and the presence of an active soft-bottom endofauna. Comparable stropheodontide assemblages lower in the Lower Leintwardine Formation, which have limited and local distribution, are restricted essentially to high energy, winnowed skeletal layers. These may represent introduced faunas or a fairly transient distribution in various shelf areas earlier in Lower Leintwardine Formation times. The major *Shaleria ornatella* fauna evidently occupied a wide tract of the shelf in late Leintwardinian times. The presence of *Calymene puellaris*, *Encrinurus stubblefieldi*, and limited occurrence in this association of the ostracode assemblage *Neobeyrichia lauensis-scissa-confluens* are important since they represent faunal immigrations (e.g. Siveter 1978; Siveter 1983).

Association D. Two further faunal associations characterized sequences of the Lower Leintwardine–lower Upper Leintwardine formations. The first of these is the *Lingula lata*—graptolite fauna of western areas of laminated siltstone facies, including thick trough sequences. The concentration of the small, thin-shelled endofaunal lingulide species in shelf edge and trough sequences (Cherns 1979, cf. epiplanktic mode of life proposed by Watkins and Berry 1977) is notable with regard to the general absence of other skeletal benthos and of endofaunal reworking, which suggests conditions inimical to most benthos. Planktic graptolites form the only other common fauna in these sequences, except in slump units where assemblages of shelly fauna were apparently derived with the sediment from outer shelf environments. Small pterineids, nautiloids, rare cardiolids, and *D. navicula* valves form minor faunal components. The thin-shelled pterineids represent epibyssate organisms; although they mostly occur as isolated valves, rare articulated specimens at Kerry and Aymestrey indicate local derivation. At this level in the sequence these bivalves are infrequent by comparison with the crowded, transported assemblages of single valves, predominantly of one type, described from the older, Wilsonia Shales formation at Builth (Straw 1937). Orthocones are mostly small, infrequent, and dispersed, although larger and aligned specimens occur in some bedding assemblages. A trough distribution is not necessarily original for these Ludlow cephalopods, though relation chiefly to an offshore 'graptolitic water mass' has been suggested (Watkins and Berry 1977; Hewitt and Watkins 1980). It is evident that the association of lingulides and graptolites represents a thanatocoenosis. The sparse and dispersed distribution of both in many sediments contrasts strongly with the rich bedding surface assemblages—if only occasional—which represent current accumulations of each or of the two together (e.g. Lyepole Bridge; Aberedw, Wood 1900).

Association E. The remaining association is the *Aegiria grayi*—ostracode faunas which characterize the high Lower–Upper Leintwardine beds in mid-shelf to trough areas. The association has a wide facies distribution; it occurs in calcareous siltstone facies, particularly the more thickly flaggy type, in the 'intermediate' facies to the latter from the laminated siltstone facies, in laminated siltstone facies, and in the poorly calcareous facies of south-western areas. To some extent this association overlaps with the *S. ornatella* shelf fauna (e.g. at Ludlow). The assemblages are typically in thin, winnowed skeletal sand layers where the small size of the grains and limited extent of deposits suggest only moderate current energy. In most areas the sediments at this level are well bioturbated, indicating an active soft-bottom endofauna. In the Builth area it is notable that the lithological change up into thickly flaggy calcareous siltstone facies follows closely upon rapid increase in bioturbation and the incoming of this fauna at the top of the laminated siltstone facies. The sequence at Shelderton shows a similar pattern, though spread over a wider interval (text-fig. 11c). However, at Kerry the association first occurs as thin skeletal sand layers among laminated siltstone facies which lack traces of bioturbation (text-fig. 12). The assemblages comprise the small brachiopod *A. grayi*, beyrichiacean and non-palaeocope ostracodes, associated with variable amounts of fine skeletal sand debris, small crinoid ossicles, trilobites, and *D. navicula*. It is arguable whether *A. grayi* represents a benthic or epiplanktic form (p. 486), but beyrichiaceans were apparently vagile benthos. With regard to the ecological significance of this association it is important to note that there is some succession in the beyrichiacean ostracode assemblages; the first occurrences at Ludlow and in shelf edge areas are of *A. grayi* with small beyrichiaceans, followed in higher beds by the incoming of the neobeyrichiid species *N. nutans*, and then by the main assemblage of *N. lauensis–scissa–confluens*. Around this same level in sequences there is also an increase in vagile benthos represented by trilobites. The distribution and composition of the association suggest a benthic epifaunal brachiopod assemblage of outer shelf environments, associated with a significant vagile arthropod skeletal benthos and with an active, largely soft-bodied soft-bottom endofauna. Its spread westwards at the *scissa–lauensis* level, mainly closely linked to lithological change to coarser sediments, suggests regional environmental shifts. Whether the distribution of algal material was an important factor either in the benthic environment or as a transporting medium, particularly in areas where benthos was otherwise scarce, cannot be assessed. The incoming of the association as skeletal sand layers into areas of fine silts which previously lacked, or had limited benthic organisms, might represent an early stage during colonization by benthic faunas (e.g. Jaanusson 1984).

PALAEOGEOGRAPHY

The faunal shifts which define the base of the Lower Leintwardine Formation in the type area correlate broadly with the transition from low to moderate energy, carbonate mud and silt depositional environments into dominantly clastic silt sedimentation (text-figs. 13A, B and 14). Similar carbonates, which Watkins and Aithie (1980) interpreted as back-barrier shelf facies, extended inshore across the shelf, and in these areas the faunal boundary is again near the top of the carbonate development. At the boundary, fairly sparse though diverse 'residual' assemblages of beds high in the Upper Bringewood Formation were replaced, with loss of a number of diagnostic fossils, mainly by articulate brachiopod assemblages of long-ranging forms. Further offshore, to the west, where the Upper Bringewood Aymestry Limestone is in high and moderate energy, carbonate sand and gravel facies that represent an outer shelf barrier belt (Watkins and Aithie 1980), the corresponding faunal changes lie well within the carbonate formation. Here, richer Bringewoodian assemblages of large recumbent brachiopods (pentameraceans, strophomenaceans) and tabulate corals in sand grade, mud- to grain-supported carbonates gave way to prolific, hard- and soft-bottom 'small' brachiopod faunas, particularly *D. navicula*, in facies of fluctuating but generally lower depositional energy levels. Clastic silt deposition soon became dominant also in these areas, although carbonate environments persisted, with some eastward shift in depositional focus, through lower energy mud- and silt-grade facies across part of the Wenlock Edge region.

The Upper Bringewood–Lower Leintwardine faunal boundary across the inshore shelf areas (i.e. as seen in the inliers) is associated widely with breaks in deposition, episodic erosion, and hardground formation, indicated by skeletal conglomerates that occur both within the Aymestry Limestone muddy carbonate belt and in laterally adjacent carbonate-rich clastic depositional zones. The latter, which extend southwards from south Woolhope, are thinner sequences in which beds of winnowed, coarse conglomeratic skeletal sand indicate episodes of raised current energy among